NEOGENE FOSSIL FISHES FROM THE LAKE ALBERT-LAKE EDWARD RIFT (ZAIRE)

GENERAL

BY PETER HUMPHRY GREENWOOD AND GORDON JON HOWES

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ABSTRACT

A large collection of fishes from Miocene, or possibly Pliocene, and Lower Pleistocene deposits in the Lake Albert-Lake Edward Rift (Zaire) is described and catalogued. Two new taxa are also described, a species of *Lates* (Centropomidae) showing several derived features in the syncranium, and a new genus and species of characoid fish whose affinities seem to be with American rather than African members of the suborder. This discovery has led to a reconsideration of the Egyptian fossil characoid *Alestes deserti* Greenwood.

Apart from these new taxa, the Miocene fish fauna of this area in the Western Rift Valley differs little from contemporaneous faunas in other parts of Africa, both north and south of the Sahara. The most noticeable difference, when comparisons are made with North African localities, is the absence of clariid and cyprinid fishes from Lower Miocene deposits in the Western Rift.

I. INTRODUCTION

THE MATERIAL which we have been privileged to study was collected principally by the Ganda-Congo expedition of 1960, and by Dr J. Lepersonne of the Musée Royal de l'Afrique Centrale on an earlier occasion, 1939–1940 (see Gautier 1970 for further details and references). Smaller collections by Dr X. Misonne (in 1958) and Dr J. de Heinzelin (in 1957) are also included.

Geographically, the sites cover the Lake Albert-Semliki-Lake Edward region (areas 5 and 6 in the map reproduced as fig. 1 in Gautier 1970), the northern region of the Semliki valley (area 3 in Gautier 1970) and an area near the southwestern shore of Lake Albert (areas 1 and 2 in Gautier 1970).

From the viewpoint of research on Quaternary fishes, this part of the Western Rift Valley is now undoubtedly the most intensively collected and studied region in all eastern Africa (Greenwood 1959). The new material extends our knowledge back to the Miocene, and substantially increases the information available on the Lower Pleistocene fish fauna of the area.

It is hardly necessary to stress the importance of a good palaeontological record when investigating the evolutionary history of the African lakes and their highly endemic fish faunas of today (Fryer & Iles 1972, Greenwood 1959, 1974a). Many earlier hypotheses put forward to explain this endemicity, the associated adaptive radiation of the fishes in each lake fauna, and their interrelationships with the faunas of other lakes, have been severely weakened by the later acquisition of good fossil records. Sadly, there is still a great dearth of such records for many of the lakes (especially Lakes Victoria, Tanganyika and Malawi). But, for the northern lakes of the Western Rift (Lakes Albert, Edward and George) the position is much better and a broad history of at least the non-cichlid fishes can be compiled for the Miocene to early Holocene periods (White 1926, Greenwood 1959, 1973a). Even for the cichlid fishes of these lakes the story is becoming clearer through evidence which can be derived from the history of the non-cichlids (Greenwood 1973a, 1974a, 1974b).

Probably the most important information derived from the fossils described in this paper concerns the Miocene fish fauna of the Albert-Edward Rift. Until now we were in complete ignorance of what this fauna might have been like. The answer is, in some respects, rather surprising. Besides what might be described as the 'expected' taxa there are two 'unexpected' elements. One is a species of the genus *Lates* (Centropomidae) showing superficial if not phyletic affinities with the endemic *Lates* species-group of Lake Tanganyika. The other is an undescribed characoid fish whose affinities are apparently closer to a lineage now confined to South America (the Serrasalminae) than to any lineage still extant in Africa. These new taxa are described and discussed below before we go on to give an annotated catalogue of all identifiable specimens obtained from the various sites.

All the material reported upon here is deposited in the Musée Royal de l'Afrique Centrale, Tervuren. Only type material is registered in this collection, with numbers lying in the range RG.17.501 to RG.17.600.

ADD R	Ridge for insertion of the	LC	Lateral commissure
	adductor mandibulae I muscle	Ν	Notch between ascending and
ADD SP	Spur for insertion of the		articular processes
	adductor mandibulae I muscle	OCS	Occipito-spinal nerve foramen
AHYF	Anterior facet for hyomandibula	OPSORBC	Anterior opening of supra-
ART P	Articular process of the		orbital laterosensory canal
	premaxilla	PAR	Parietal
ASC P	Ascending process of the	PHYF	Posterior facet for
	premaxilla		hyomandibula
BOC	Basioccipital	PMAXP	Posterior maxillary process
BSP	Basisphenoid	PMXP	Premaxillary process of the
Cl	Cleft between ascending and		maxilla
	articular processes	PRO	Prootic
D PROC	Dorsal process of the maxilla	PS	Parasphenoid
E	Mesethmoid	PSGR	Groove in parasphenoid
EPI	Epiotic	PTO	Pterotic
EXO	Exoccipital	PTF	Post-temporal fossa
F	Foramen in articular process	PTS	Pterosphenoid
FR	Frontal	RA	Retroarticular
FRR	Frontal ridge	SPO	Autosphenotic
GR	Groove	V	Vomer
IC	Intercalar	VS	Vomerine spine
LATE	Lateral ethmoid	IX	Foramen for glossopharyngeal
LATSGR	Laterosensory canal groove		nerve
LAT SP	Pores to laterosensory canal	X	Foramen for vagus nerve

Abbreviations used in the text figures:

11. NEW SPECIES OF FISH FROM THE MIOCENE AND EARLY PLEISTOCENE OF THE LAKE ALBERT-LAKE EDWARD RIFT

Superorder ACANTHOPTERYGII Order PERCIFORMES Family **CENTROPOMIDAE** Lates rhachirhinchus sp. nov.

(Figs 1-21)

MATERIAL AND LOCALITY. The material on which this new taxon is based comprises numerous but invariably incomplete and often fragmentary bones from the syncranium and vertebral column. It was obtained from sites situated within an area of about 1.5 km^2 in the Sinda-Mohari region of the lower Semliki valley (Hooijer *et al.* 1963: fig. 5). The principal sites are in the basal Sinda Beds at Ongoliba (collected by X. Misonne) and at Sinda-Mohari, points 1, 2 and 10 of the Ganda-Congo expedition, 1960 (Gautier 1965, 1970). (Additional specimens which were not used in this description, except indirectly to check various characters, are listed in the review of sites on pp. 106–119).

AGE. There is some uncertainty about the precise age of the basal Sinda Beds, from which the majority of *L. rhachirhinchus* remains were recovered (Gautier 1970:69-76). Published evidence suggests an uppermost Pliocene or early Pleistocene (Lower Villafranchian) age (Gautier 1970:73). However, preliminary unpublished results stemming from a revision of the mammalian fauna indicate the possibility of an early Pliocene dating (Dr J. Lepersonne *in litt.*, referring to the work of Dr C. T. Madden, University of Michigan).

HOLOTYPE. A vomer (Fig. 6A) with an almost complete spine; from Sinda-Mohari Point 10 (Ongoliba Bone Beds, base of Sinda Beds – earlier Pleistocene; see p. 112) (Hooijer 1970, Lepersonne 1970). RG.17.501.

PARATYPES. (The sites are given in brackets, after a brief description of each specimen):

Neurocranial material

- Occipital region of skull, extending from the anterior margin of the prootic to the basioccipital facet; II cm long; (basal Sinda Bone Beds, Ridge I). RG.17.502.
- 2. Damaged occipital and posterior orbital region of skull; (basal Sinda Bone Beds, Ridge 1). RG.17.503.
- 3. Specimen similar to above, but rather distorted; (basal Sinda Bone Beds, Ridge 1). RG.17.504.
- 4. Incomplete occiput from a smaller fish than those previously listed; (basal Sinda Bone Beds, Ridge 1). RG.17.505.
- 5. Incomplete otico-occipital region, slightly compressed; (basal Sinda Bone Beds, Ridge 1). RG.17.506.
- 6. Otico-occipital region, not distorted, and comprising about the same region of the skull as specimen 1; (basal Sinda Bone Beds, Ridge 1). RG.17.507.

- 7. Otico-occipital region of the skull from a large fish, rather damaged; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.524.
- 8. Fragment of neurocranium, comprising part of the otic region, with roofing bones but no parasphenoid; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.508.
- 9. Almost complete skull, although damaged and compressed in places ; (Ongoliba bone bed, basal Sinda). RG.17.509.
- 10. Vomer; 3 specimens in which the tooth patch is 18 mm (f1) or 19 mm (f2) across; (basal Sinda Bone Beds, Sinda-Mohari, point 2). RG.17.510-512.
- Vomer; II specimens, variously damaged; width of tooth patch on largest specimen c 25 mm, and c I3 mm on the smallest; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.513-523.
- 12. Anterior part of the dorsicranium, together with the ethmoid region; (basal Sinda Bone Beds, Sinda-Mohari, Ridge 1). RG.17.525.

Jaws, Palatoquadrate arch, etc.

- 13. Premaxillae ; 14 specimens, variously damaged, 6 left and 8 right ; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.526-539.
- 14. Dentary ; almost complete left ramus (length from symphysis to angle between ascending and horizontal arms 114 mm) ; (basal Sinda Bone Beds, Sinda-Mohari, point 1, ridge 1). RG.17.540.
- 15. Dentary ; 27 fragmentary specimens ; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.541-567.
- 16. Quadrate; 2 fragments, comprising the articulatory surface; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.568-569.
- 17. Quadrate ; somewhat damaged but comprising the articulatory surface and part of the body ; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.570.
- 18. Quadrate ; damaged, right ; (basal Sinda Bone Beds, Sinda-Mohari, point 2). RG.17.571.
- 19. Premaxillae, one left, one right; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.572.
- 20. Dentary; about the anterior half of left ramus; (basal Sinda Bone Beds, Sinda-Mohari, point 2). RG.17.573.
- 21. Premaxillae ; one left, one right ; (Karugamania, Lower Miocene ; coll. J. de Heinzelin). RG.17.574.
- 22. Maxillae; 3 (1 left, 2 right), variously damaged; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.575-577.
- 23. Angulo-articular; 12 damaged specimens; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.578-589.
- 24. Angulo-articular ; one right, from skull about 18 cm long ; (basal Sinda Bone Beds, Ridge 1, basin B). RG.17.590.
- 25. Angulo-articular with attached retroarticular, right; (Ongoliba Bone Bed, basal Sinda). RG.17.591.
- 26. Autopalatine, left, anterior part only; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.592.

- 27. Autopalatine, right ; the anterior region but with a small part of the associated tooth-bearing dermopalatine ; (basal Sinda Bone Beds, Sinda-Mohari, point 5). RG.17.593.
- Vertebrae
- 28. First abdominal; width of anterior face 25.5 mm, of posterior face 30.5 mm; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.594.
- 29. Third abdominal; width of anterior face 39.0 mm, of posterior face 42.0 mm; (basal Sinda Bone Beds, Ridge 1). RG.17.595.
- 30. ? Fourth-fifth abdominal ; width of anterior face 24.0 mm, of posterior face 26.0 mm ; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.596.
- 31. Posterior abdominal (position indeterminable) ; width of anterior face 47.0 mm, least width of centrum 40.0 mm ; (basal Sinda Bone Bed, point 10). RG.17.597.
- 32. Caudal (position indeterminable); width of anterior face 13.5 mm, width of posterior face 13.0 mm, length of centrum 16.0 mm, least width of centrum 8.0 mm; (basal Sinda Bone Bed, Sinda-Mohari, point 10). RG.17.598.

ETYMOLOGY. The specific name *rhachirhinchus* is derived from the Greek $\dot{\rho} \dot{a} \chi \iota s$ a spine, and $\dot{\rho} \hat{\iota} \iota \epsilon s$ a snout. It refers to the peculiar spine-like process on the vomer (p. 83).

SIZE RANGE. It is difficult to estimate from such fragmentary material the size of the fishes represented. Basing our estimates on the size of certain neurocranial bones and on the dimensions of vertebral centra as compared with similar bones in the skeleton of extant *Lates niloticus* and *L. calcarifer*, the size range of the *L. rhachirhinchus* represented is from c_{30} to c_{200} cm standard length.

DIAGNOSIS. Lates rhachirhinchus differs from all living species of the genus principally in having a forwardly projecting median spine on the vomer (p. 8_3); by peculiarities in the shape of the premaxilla, maxilla and articular (pp. 86, 85, 88 respectively); in having a narrow and ventrally convex parasphenoid with a deep median groove on its posterior third (p. 8_2), a shallow post-temporal fossa that does not open into the cranial cavity (p. 77), a broad lateral commissure (p. 80), frontal ridges that extend far anteriorly and then fuse medially (p. 77); by differences in the shape of the autopalatine (p. 85); and by several differences in the morphology of the first and third to seventh abdominal vertebrae (pp. 81-85). Other differential characters are discussed below.

Where these features can be compared with their counterparts in other fossil *Lates*, they are also diagnostic (see review of fossil *Lates* species by Sorbini 1973). An exception is provided by the palatine of *L. rhachirhinchus*, which is virtually identical with a palatine from the Pliocene deposits of Wadi Natrun, Egypt (p. 85; Greenwood 1972). The other *Lates* material from Wadi Natrun, however, shows typical *L. niloticus*-like characteristics.

NEUROCRANIUM. Judged on the abundant though incomplete skull material, the neurocranium of L. *rhachirhinchus* is narrower than that of any extant African centropomid, especially in the preorbital and interorbital regions and in the posterior

otic region. It also has a lower vault, and lower, but stouter and anteriorly more extensive, fronto-parietal ridges. Other unique features are the vomerine spine, the poorly developed post-temporal fossa and the relatively more elongate oticooccipital region.

Narrowing of the preorbital skull, and especially of the lateral ethmoids, has apparently led to the loss of a foramen for the olfactory nerve and blood vessel in these bones. This feature, together with the vomerine spine and the imperforate post-temporal fossa, is unique within the genus and, apparently, within the Centropomidae as a whole. All must be ranked as derived, i.e. apomorph, features.

In the detailed description below, all comparisons with extant species of *Lates* should be taken to include comparison with the monotypic genus *Luciolates stappersi* whose neurocranial architecture is essentially like that of *Lates*.

DORSIGRANIUM. The skull roof is narrow, the width across its otic region being only a little greater (about $1\frac{1}{2}$ times) than at the exoccipital condyles. Expressed in another way, the maximum breadth of an entire *L. niloticus* skull 12.5 cm long is about equal to that of an incomplete fossil neurocranium measuring 11 cm from the basioccipital facet to the anterior point of the prootic.

The frontals and parietals have prominent and robust crests, those of the frontals extending forward to a point level with the anterior opening of the supraorbital lateral-line canal, i.e. almost to the posterior part of the ethmofrontal suture. Over the anterior part of their course the frontal ridges of each side are at first parallel to one another, but then become closely apposed. Shortly after that point the ridges fuse and disappear (Fig. I; cf. Fig. 5A, B).

The first opening to the supraorbital lateral-line canal is large and lies in a deep gutter. Somewhat posteriorly is another opening to this canal lying in a high and A-shaped coaming of bone that extends antero-laterally at an angle to the frontal ridge with which it merges medially (Fig. 5). Judged on the only specimen in which the frontals roofing the orbit are preserved

Judged on the only specimen in which the frontals roofing the orbit are preserved (p. 000), the fossil has extremely narrow preorbital and interorbital regions, narrower even than in *Luciolates*. This narrowness is partly due to the narrow frontals but also results from the lateral ethmoids not being laterally expanded.

In no specimen is the supraoccipital crest complete, so its height cannot be determined. However, in two specimens the bone's anterior extension is probably determinable. In one specimen it seems not to extend forward beyond a point level with the middle of the sphenotic; in the other it reaches a point level with the midpoint of the hyomandibular facet in the pterotic. All extant *Lates* species have the supraoccipital extending forward beyond these points (Fig. 1A); it is least extensive in *L. calcarifer*.

The post-temporal fossa is a shallow, rather elongate depression with a complete bony floor (Fig. 4). In this respect *L. rhachirhinchus* contrasts strongly with all extant *Lates* species. In these taxa the fossa is a clearly circumscribed and deep cavity with a medioventral opening into the brain case, closed in life by a tough membrane. Even in *Luciolates*, where the fossa is shallower than in *Lates*, it is perforate and far more definite than in *L. rhachirhinchus*.





FIG. I. Lates niloticus. Neurocranium. A. Dorsal view. B. Left lateral view.

All lateral line canals on the skull roof are bone-enclosed.

ORBITAL, OTIC AND OCCIPITAL SKULL REGIONS. The pterosphenoid is an expansive bone extending forward into the orbit and coming into broad and close contact ventrally with the prootic (Figs 2, 3). Unfortunately in no specimen is it possible to see clearly the exact relationships between the prootic, pterosphenoid and parasphenoid. In extant species there are clear-cut interspecific and ontogenetic differences in this posterior region of the orbit. Some species (e.g. *Lates calcarifer, L. niloticus, L. angustifrons*) have a distinct pterosphenoid pedicle which provides a tunnel for the oculomotor and profundus nerves, and the internal jugular vein. Others, including *Luciolates*, have no pedicular tunnel, the nerves and blood vessel being bridged only by a narrow ligamentous or osseous arch (Greenwood, unpublished). Correlated with this latter condition, the pterosphenoid is relatively foreshortened and not expansive as it is in L. *rhachirhinchus* and those species with a pedicular tunnel. However, an expansive pterosphenoid does not necessarily imply the development of a tunnel and thus it cannot be concluded that one existed in L. *rhachirhinchus*.

In *L. rhachirhinchus*, unlike any extant *Lates* species, the ascending parasphenoid wing, which meets the prootic, rises in a gentle slope, not a pronounced step, and there is a corresponding antero-ventral prolongation of the prootic (Fig. 2A). Also unlike the condition in living species is the relatively acute angle formed by the sphenotic and prootic bones where they meet, lateral to the anterior opening of the trigemino-facialis chamber (Fig. 2A).



FIG. 2. Lates rhachirhinchus. Otico-occipital region of the skull. A. Right lateral aspect. B. Ventral view. (Paratype RG.17.502.) Unstippled areas represent adherent matrix.

The sphenotic, immediately anterior and dorsal to its suture with the prootic, is deeply excavated so as almost to mirror the anterior hyomandibular facet (Figs 2, 3). In all other respects the sphenotic does not differ greatly from the condition found in living species.

The prootic, in its general outline, does not depart markedly from that bone in other *Lates* species, but see above with regard to its contact with the parasphenoid. The lateral commissure, however, is relatively much wider in *L. rhachirhinchus*, and the openings to the trigemino-facialis chamber are apparently larger (Figs 2, 3).

Both the anterior and posterior cranial facets for the hyomandibula are welldefined, the anterior one (in the prootic and sphenotic) is a deep, hemispherical pit, the posterior one a relatively shallow and elongate groove on the pterotic.



FIG. 3. Lates rhachirhinchus. Otico-occipital region of the skull in right lateral view. (Paratype RG.17.507.) Unstippled areas represent adherent matrix.

Compared with most extant species, the otic region in *L. rhachirhinchus* is narrower and shows none of the slight inflation generally characterizing the anterior and ventral regions of this part of the skull; in this respect *L. rhachirhinchus* resembles *Luciolates* and *L. angustifrons* rather more closely.

A deep groove on the exoccipital runs obliquely antero-ventrally, from the large vagus and smaller glossopharyngeal nerve foramina (Fig. 4). Below this groove the area of the exoccipital bordered ventrally by the suture with the basioccipital, and posteriorly by the buttress of the facet, is concave like the same area in extant species. The exoccipital facets are apparently circular in outline (kidney-shaped in other species), but each has a medially directed, tab-like projection that meets its counterpart in the midline below the foramen magnum. A large nerve foramen penetrates the upper surface of the prominent buttress leading to the facet (Fig. 2A).

The basioccipital has the same proportions and morphology as in all extant species, although the facets for Baudelot's ligament seem somewhat deeper. When



FIG. 4. Lates rhachirhinchus. Occipital region of the skull, in right lateral view, to show the complete bony floor to the post-temporal fossa. (Paratype RG.17.506.)

the skull is viewed laterally the ventral surface of the basioccipital and underlying parasphenoid slopes gently but noticeably upwards, passing back from a point vertically below the hind margin of the anterior hyomandibular facet (Fig. 2A). A similar inclination, but starting further forward, is seen in *L. mariae*, *L. microlepis* and *Luciolates stappersi*; all other living species have this region of the skull in virtually the same line as the anterior part of the parasphenoid (cf. Fig. 1B with Fig. 2A).

Without an entire neurocranium it is impossible to form a precise opinion about the proportions of the otico-occipital region. Its narrowness has been noted already. If comparable-sized specimens of *L. calcarifer* and *L. niloticus* are compared with *L. rhachirhinchus*, then the otic region (exoccipital to the anterior prootic border) of the latter is relatively more elongate. As the only available skeletons of other *Lates* species and of *Luciolates stappersi* are much smaller than any fossil skull, a direct comparison is not feasible. However, the otic region in *L. rhachirhinchus* gives the impression of relative elongation, except possibly when compared with *Luciolates*. Another impression is that the cranial vault in *L. rhachirhinchus* is lower and flatter than in other species, and that this is attributable to a relative decrease in the depth of those bones lying above the level of the hyomandibular facets.

PARASPHENOID. Throughout its length, the ventral surface of the parasphenoid is rounded in the transverse plane, especially in the orbital region. Below the otic region the parasphenoid has a slightly flatter cross-section, and is marked by a deep and broad median groove which is almost continuous with a shorter and narrower groove in the basioccipital. The parasphenoid groove terminates anteriorly at a point immediately below the lateral commissure (Fig. 2).

The rounded cross-section and the median groove are characters not found in the parasphenoid of any extant *Lates* species.

ETHMO-VOMERINE REGION. The description of this region is based mainly on one specimen, the only one in the whole collection showing a relatively undamaged ethmoid complex (Fig. 5). The vomer, however, is represented by several almost intact bones (Figs 6, 7).



FIG. 5. Lates rhachirhinchus. Ethmoid and anterior frontal region of the skull. A. Slightly oblique dorso-lateral view of the left side. B. Dorsal view. (Paratype RG.17.525.)



FIG. 6. Lates rhachirhinchus. Vomers. A and B. Left lateral views. C. Ventral view of B. A and B show variation in the angle of the vomerine spine; in B this process is broken but in A it is almost complete. (Fig. 6A is the holotype; other specimen from paratype lot RG.17.513-524.)

The vomer is a most characteristic element, quite unlike that found in any extant species, despite its basic similarity in shape. The median crest, instead of sloping gently upwards and backwards, is inclined forwards and resembles a laterally compressed horn (Fig. 7). There appears to be some intraspecific variability in the angle made by the horn to the body of the vomer. In some specimens the horn is almost horizontally aligned but in others it slopes upwards at an angle of c 45 degrees to the horizontal (Fig. 6). No specimen has the upper surface of the horn entire and thus it is difficult to determine how or where the ethmoid joins the process. In extant species the ethmoid suture is almost vertical, with the median crest of the ethmoid becoming continuous with the vomerine crest. The only fossil ethmoid available is damaged antero-ventrally, but judged on its general orientation it seems likely that the ethmo-vomerine suture was horizontally aligned. If this were so, then the ethmoid crest would join the vomerine horn to produce an ethmo-vomerine ridge projecting forward above and in advance of the body of the vomer.

A distinct furrow separates the vomerine crest from the body of the bone, the lateral margin of each furrow continuing forwards and downwards as a ridge over the anterior peak of the bone (Fig. 6A, B). Anteriorly, and between the ridges of each side, the vomer has a blunt, almost flat, entry angle.

The vomerine tooth patch is delimited by a distinct shelf from the edge of the vomer itself. This gives it the appearance of a plate fused with the vomer rather than, as in living species, of being an integral part of the bone (Fig. 6C). There is

considerable individual variability in the shape of the vomerine tooth patch, even amongst specimens from one site; apparently this variability is in no way correlated with size (see Fig. 7). The posterior margin of a tooth patch may be straight, slightly concave or produced into a low peak. The anterior outline varies from near-circular through cardiform to a laterally elongate near-rhomboid. There is a well-defined facet for articulation with the palatine situated above and

There is a well-defined facet for articulation with the palatine situated above and immediately behind each of the lateral projections from the vomerine body. The shaft of the vomer, in its shape and proportions, is like that in living species.



FIG. 7. Lates rhachirhinchus. Vomers, in ventral view, to show variation in the shape of the tooth patch.

Information on the ethmoid complex is derived exclusively from a single specimen (Fig. 5) comprising the greater part of the ethmoid, the left lateral ethmoid (virtually intact save for the lateral projection that articulates with the lachrymal bone) and the supraorbital and immediately postorbital parts of the left frontal. Except for a narrow strip along the midline, the right frontal is destroyed. We estimate that these bones are from a skull c 12 cm long.

The mesethmoid differs little from that in extant species, apart from its marked lateral compression, in which feature, as might be expected, it resembles *Luciolates stappersi*, another narrow-skulled form. Also, in *L. rhachirhinchus* the two dorsal projections underlying the dermethmoid are, as compared with all living forms, reduced to mere laterally directed and low ridges with no forward projection at all. In extant taxa the projections are horn-like and extend forward well beyond the outline of the median ethmoidal ridge.

The lateral ethmoid compares closely with that bone in *L. niloticus* except that it is much less extensive laterally and does not stand away from the skull as a distinct bony shelf. In this respect *L. rhachirhinchus* differs markedly from *Luciolates* and the endemic Lake Tanganyika species of *Lates*. In these the lateral ethmoid not only extends laterally but also downwards and backwards, giving the appearance in lateral view of a solid triangular wedge linking the vomer with the orbital margin.

No trace could be found of a foramen for the olfactory nerve, nor is there any indication that it might have been destroyed. Instead, in this region of the ethmoid there is a shallow, blind pit on the orbital side of the bone. Presumably the narrow ethmoid in *L. rhachirhinchus* obviates the need for a foramen, and the olfactory nerve therefore would pass directly from the orbit onto the lateral face of the ethmoid.

PALATOPTERYGOID ARCH. This complex is represented by two palatines only. In several details the autopalatine of L. rhachirhinchus differs from that of all extant *Lates* species. The most obvious difference lies in the shape and orientation of the maxillary process (Fig. 8) which, in the fossil, is more sharply angled relative to the dentigerous surface. As a result the process lies almost parallel to the dentigerous surface. Furthermore, the ridge from which the process arises is more prominent and, anteriorly, there is a distinct shoulder of bone extending medially and somewhat posteriorly from the base of the process. Compared with that in extant species, the dorsal facet of the maxillary process is poorly defined and lies further dorsally; the ventral vomerine facet, although well-defined, is smaller and directed further ventrally in L. rhachirhinchus than in the extant species.



FIG. 8. Palatines (right) of: A and C. L. rhachirhinchus (paratype RG.17.593); B and D. L. niloticus for comparison. A, B dorsal views; C, D medial views.

In all these features the autopalatine of L. *rhachirhinchus* closely resembles that bone in an unnamed *Lates* species from the Pliocene of Wadi Natrun (Greenwood 1972 : fig. 2).

UPPER AND LOWER JAWS. *Maxilla* (Figs 9, 10). No entire maxilla is preserved but there is a sufficiently large number of maxillary heads to show that this end of the bone differs in several respects from the maxilla in other species of *Lates* and in *Luciolates*.

In L. rhachirhinchus the dorsal process, for articulation with the ethmoid-vomer, is relatively higher and more rectangular in outline. The premaxillary process differs in having a less well-defined articulatory process on the portion directed ventro-medially, which in turn is separated from the dorsal portion by a deeper and

more distinct groove (Fig. 9) running laterally at an angle of c 45 degrees. In extant species this groove is horizontal. Another difference in the premaxillary process is the way in which it is drawn out into a lip-like projection; in extant species this region does not extend forwards beyond the dorsal part of the process, and the articulatory surface is larger and more clearly circumscribed (Fig. 9). A survey of the premaxillary process in extant *Lates* species (including *Luciolates stappersi*) also shows that this articulatory process is vertically or almost vertically inclined, whereas in *L. rhachirhinchus* it lies almost horizontally.

Behind the maxillary head, and immediately posterior to the saddle on which the palatine articulates, there is a very prominent spur of bone to which could have been attached the tendon for the *adductor mandibulae* I muscle. No extant species has such a well-developed process; in these fishes it has the form of a low ridge (Fig. 10).

Premaxilla. In *L. rhachirhinchus* this bone is also distinctive. Again there are no complete specimens, but several fragments from the dentigerous area and anterior region are preserved. The description which follows is concerned only with the anterior region of the bone since it alone shows diagnostic features.



FIG. 9. Maxillae. Anterior view of the left maxillary head in : A. L. niloticus, and B. L. nhachirhinchus (from paratype lot RG.17.575-577).



FIG. 10. Maxillae. Lateral aspect of left maxilla in : A. L. niloticus, and B. L. rhachirhinchus, to show the spur for attachment of the adductor mandibulae I muscle (from paratype lot RG.17.575).

When viewed laterally, the dentigerous surface, unlike that in extant species, is not continued forwards to form a narrow ledge skirting the anterior face of the bone (Figs II, I2). Instead, it fails to project beyond the anterior margin. The articular process in *L. rhachirhinchus* is larger, especially broader, than in extant species. When seen from above, it lies at an angle to the ascending process (not in the same line) and is inclined medially (not vertically as in the living species). Extant *Lates* and *Luciolates* have a discrete median arm extending inwards from the lateral, shield-like portion of the articular process. In *L. rhachirhinchus* this arm is barely represented by a low basal ridge (Fig. 12).



FIG. 11. Premaxillae of : A. L. niloticus in left lateral view ; B. L. rhachirhinchus in right lateral view ; C. L. rhachirhinchus, anterior part of premaxilla showing ascending and articular processes, and the foramen in the latter. (Specimens figured in B and C are from paratype lot RG.17.572.)

The stout ascending process is inclined somewhat forwards in L. rhachirhinchus, but in other species it is bowed and curves gently backwards. In all extant species, including *Luciolates stappersi*, the process is more slender and is separated from the articular process by a deep but narrow cleft extending almost to the bases of the two processes. *Lates rhachirhinchus*, in contrast, has the articular process fused to the ascending process over the greater part of its length; a shallow notch, slightly below the tip of the articular process, is all that remains of the cleft (Fig. II). A unique feature of the premaxilla in L. rhachirhinchus is a large foramen that opens



FIG. 12. Premaxillae of: A. L. niloticus, and B. L. rhachirhinchus (from paratype lot RG.17.572). In both, the anterior end of the bone is seen from above to show the relationship of the articular and ascending processes.

medially below the notch, then passes obliquely downwards and opens laterally near the base of the articular process. No trace of this foramen is found in any living species; presumably in *L. rhachirhinchus* it provided a passage for a branch of the maxillary nerve and perhaps also for a blood vessel. In *Lates niloticus* a large blood vessel passes through the cleft between the ascending and articular processes, and several nerves pass outwards and downwards on the lateral face of the premaxilla.

No specimen of a *L. rhachirhinchus* premaxilla is sufficiently complete for us to determine accurately the size of the posterior maxillary process; where some of the process is preserved it seems to be lower than in other species.

No bone can be identified as a supramaxilla.

Dentary. Unlike the jaw bones described so far, the dentary in *L. rhachirhinchus* seems to depart but slightly from that bone in extant species. The only differences we could detect are the relatively longer openings to the lateral-line sensory canal and a relatively narrower dentigerous surface (Fig. 13). It must, however, be remembered that only the anterior portion of the dentary is preserved in our specimens.

As with the premaxilla, the pattern of densely packed and small bones of attachment on the dentary suggests that the teeth and dental pattern were similar to those in living *Lates* species. Certainly there are no indications of an outer row of enlarged teeth like those on the dentary of *Luciolates stappersi*, nor of the few enlarged anterior premaxillary teeth such as occur in the premaxilla of that species.

Angulo-articular. Most specimens are incomplete, and comprise only that area of the bone around and forming the articulatory facet for the quadrate head. Compared with the angulo-articular in other *Lates* species, that of *L. rhachirhinchus* has a deeper facet, distinctly bowl-shaped in lateral outline, with the posterior face rising more steeply, almost at a right angle, and its tip curving anteriorly (Fig. 14).



FIG. 13. Dentaries of : A and B. L. niloticus, occlusal and left lateral views respectively; C and D. L. rhachirhinchus, occlusal and left lateral views (paratype RG.17.540).

Also, the groove for the latero-sensory canal which underlies the facet is deeper and longer in this species.

Retroarticular. This is present in two specimens; it is a stout and relatively triangular bone, differing in these respects from the larger and less regularly shaped retroarticular in all extant species except L. *calcarifer.* In that species the bone does resemble the retroarticular of L. *rhachirhinchus.*

Quadrate. In L. rhachirhinchus (Fig. 15) this is very similar to the quadrate in all other Lates species, except that the articulatory head and the adjacent anteroventral limb of the bone slope ventromedially at an appreciable angle, being horizontal in other species.

SUSPENSORIUM, OPERCULAR AND BRANCHIAL SKELETONS. Apart from several gill rakers and one bone tentatively identified as an epihyal, no recognizable elements of these skeletal systems are represented in the collections. The gill rakers are of



FIG. 14. Angulo-articulars, right bone in lateral view, of: A and B. L. rhachirhinchus; C. L. niloticus. The retroarticular is present in A and C. (Specimens shown in A and B are paratypes RG.17.591 and 17.590 respectively.)



FIG. 15. Quadrates. Anterior aspect of right quadrate in : A. L. rhachirhinchus (paratype RG.17.570), and B. L. niloticus (outline only), to show differences in the shape of the articular surface.

the elongate type which forms the outer row of rakers on the first gill arch in extant species. The fossil rakers closely resemble those in L. *niloticus*, but appear to be relatively wider at the base.

The presumed epihyal is a fragment that may be the posterior half of that bone. It differs quite markedly from the epihyal of extant *Lates* in several features, including its thickness, the concavity in its posterior ventral outline (straight or convex in other species) and in details of the presumed articular surface for the interhyal.

Reference can be made here to several fragments of bone which, from their general morphology, may be branchiostegal rays. Since these bones are mere fragments, and because they differ in several small details from the branchiostegal rays of living *Lates* species, our identification must be considered as very tentative.

VERTEBRAL COLUMN. Almost without exception, the vertebrae in this collection consist of damaged centra. The few exceptional specimens have the neural or haemal arch, or both, still attached but in none is the entire neural or haemal spine preserved.

Apart from the first and third abdominal vertebrae, it is difficult to establish the exact position of a centrum in the column. This difficulty is due in part to the results of damage and in part to morphological differences existing between the fossil centra and those of extant species. We have, therefore, attempted to identify and describe only the first six abdominal centra. The presumed position of these elements has been arrived at on the basis of overall similarity between a fossil specimen and a particular vertebra in the extant species. When dealing with centra posterior to the third we have placed special emphasis on the socket in which the pleural rib articulates.

The peculiar overall morphology of the first and third centra is shared by fossil and living species, thus making the identification of these elements quite definite. No centrum is identified as being from the second abdominal vertebra of *L. rhachirhinchus*. One centropomid second vertebra is, however, recorded from Sinda-Mohari Point 6. The deposits here are considerably younger than those yielding the type specimens of *L. rhachirhinchus*, and it is interesting to note that most of the *Lates* remains from Point 6 are attributable to a species close to, if not identical with, *Lates niloticus* (see p. 115). The second vertebra, too, is indistinguishable from that of *L. niloticus*.

First vertebra (Fig. 16). There is some intraspecific variability in the shape of the centrum. Many specimens have the centrum clearly shorter ventrally than dorsally, i.e. when it is viewed laterally it tapers gradually from top to bottom. The width of the anterior face is but slightly greater than its depth, and the trabeculae running from the exoccipital facets are tightly arranged and extend obliquely across the entire length of the centrum.

Variants of this common type include centra of almost uniform length dorsally and ventrally, others with loosely arranged trabeculae immediately below the facet which merge imperceptibly with those on the body of the centrum, and, less



FIG. 16. Lates rhachirhinchus. First abdominal vertebra in : A. anterior, and B. left lateral views. (Paratype RG.17.594.)

frequently, some centra that are noticeably wider than deep (i.e. about $I\frac{1}{2}$ times, as compared with I to $I\frac{1}{3}$ times in the others).

Whatever the characters of the central body, its exoccipital facets have a constant and characteristic form. They are confluent medially, with the zone of contact thrown upwards into a saddle-shaped area projecting well above the plane of the facets. Only in *L. calcarifer* and *L. microlepis* amongst extant species does one find a condition approaching that in *L. rhachirhinchus*. The first vertebra of *L. rhachirhinchus*, however, differs from that in all other *Lates* species in having a relativlye smaller facet area. As a result of this reduction in size, a vertical dropped from the posterior rim of the facet falls just behind the anterior face of the centrum and not,



FIG. 17. Lates rhachirhinchus. Third abdominal vertebra in : A. anterior, and B. right lateral views. (Paratype RG.17.595.)



FIG. 18. Lates rhachirhinchus. Fourth or fifth abdominal vertebra in : A. anterior, and B. left lateral views. (Paratype RG.17.596.)

as in other species, to a point near the middle of the centrum or even a little further posteriorly. The angle of inclination on the facets is similar in all species, including *Luciolates*.

Third vertebra (Fig. 17). The proportions of this centrum, which is somewhat compressed antero-posteriorly, are like those in extant species. However, the anterior face is more concave and lacks the narrow but prominent collar of bone lying concentrically and immediately within the bevelled outer margin. The posterior face has about the same degree of concavity in L. rhachirhinchus and the living species, although in the former the margin is more distinctly bevelled, and there is a broad, concentric ridge surrounding the concavity. In other words, the situation on the posterior face in L. rhachirhinchus vertebrae is like that on the anterior face in extant species.



FIG. 19. Lates rhachirhinchus. Fourth or fifth abdominal vertebra in right lateral view, to show variability in this centrum. A non-typical specimen ; compare Fig. 18.

The prezygapophyses are well-developed, and the deep glenoid facet for the pleural rib lies immediately below the bony brace extending between the pre- and postzygapophyses.

Fourth or fifth vertebrae (Figs 18 and 19). No more precise location can be determined for centra assigned to this position in the column. This uncertainty is because the fossil centra do not resemble at all closely their presumed counterparts in extant species. The centra are assigned to a 'fourth-fifth' position because they have the rib facet situated ventro-laterally, and because there is no trace of an incipient 'transverse process' such as occurs on the sixth and seventh vertebrae in extant species.

In extant species the rib facet on the fourth vertebra lies high on the centrum, occupying about the anterior half of its dorsal moiety. The fifth vertebra in these species has the facet placed much lower down, almost entering the ventral outline of the centrum.

The facet occupies a ventro-lateral position in all the L. rhachirhinchus centra assigned to a 'fourth-fifth' position. Its lower margin is produced to form a distinct gutter-like lip, a feature not observed in any extant species. Amongst our specimens there is some variation in the extent to which the lip is developed, and a correlated variation in the position of the facet. Those centra with the more ventral facet are presumed to be the fifth vertebra.

If our specimens represent a mixture of both fourth and fifth centra then the situation in *L. rhachirhinchus* is quite unlike that in any other species of the genus, not only in the details noted above but also in having the two vertebrae so similar. But the likelihood of these centra being mostly or even entirely from fourth vertebrae is indicated by a specimen of two centra still in articulation. One member of this pair is of the type we identify as a third vertebra ; the other closely resembles the majority of centra classified in the category 'fourth or fifth'. Thus, either the fifth vertebra is represented by those centra which differ slightly from the modal type, or else the centra we have tentatively identified as the 'sixth and seventh' are in fact the fifth and sixth vertebra respectively.

Be that as it may, there are indications that the centrum of the 'fourth or fifth' vertebra shows size-correlated changes in proportions. The three smallest specimens (breadth of anterior face 11.0, 12.0 and 14.0 mm; length of centrum 10.0, 10.0 and 12.0 mm respectively) have proportions like those of similar-sized fifth centra in *L. niloticus*. Larger centra, however, are relatively broader (i.e. breadth 23.0, 30.0, 33.0 and 36.0 mm; length 14.0, 22.0, 18.0 and 22.0 mm for the centra respectively), and differ similarly from centra in *L. niloticus* of comparable size. Full comparison with other *Lates* species and with *Luciolates* is precluded by the absence of large specimens of these species.

? Sixth vertebra. The one relatively undamaged specimen on which this description is based has small 'transverse processes', first seen on the sixth vertebra of L. niloticus and all other species, hence our identification of the fossil as being that vertebra. The rib facet is small and lies above and behind the transverse process.

? Seventh vertebra (Fig. 20A). The 'transverse process' on this centrum is but slightly better developed, although the rib facet has virtually disappeared.

Other abdominal and caudal vertebrae. Since it is impossible to determine column position for these centra, they cannot be compared directly with their counterparts in extant *Lates* and *Luciolates* species.

Two morphotypes are represented in the collection. One (Fig. 21) has the appearance and proportions of posterior abdominal and caudal vertebrae in *L. niloticus*, *L. calcarifer*, *L. macrophthalmus*, *L. angustifrons* and *L. microlepis*, and of the posterior abdominal and anterior caudal vertebrae only in *L. mariae*. Luciolates stappersi is not mentioned here because all its posterior abdominal and caudal centra have a characteristically elongate form as, indeed, do the anterior abdominal centra as well.



FIG. 20. Lates rhachirhinchus. A. ? Seventh abdominal vertebra in right lateral view, non-typical specimen. B. ? Eighth abdominal vertebra, in right lateral view, non-typical specimen. C. Posterior caudal vertebra (elongate type) in (i) anterior and (ii) right lateral views, non-typical specimen.

The second type of fossil centrum (Fig. 20C) is more elongate, with a distinctly compressed middle section that gives it a waisted, almost hourglass-shaped outline. They closely resemble the posterior caudal centra of *L. mariae* and all caudal centra in *Luciolates stappersi*.



FIG. 21. Lates rhachirhinchus. Posterior abdominal vertebra in: A. anterior, and B. left lateral views. (Paratype RG.17.597.)

From this we conclude that there is in *L. rhachirhinchus* a gradient of centrum shape and proportions like that in *L. mariae* amongst extant forms. It may be noted in this connection that, relative to species in the *L. niloticus* complex, *L. microlepis* of Lake Tanganyika has somewhat more elongate caudal centra, particularly in the middle section of that region in the column. This differentiation, like that found in the other Lake Tanganyika species *L. mariae* and *Luciolates stappersi*, may be correlated with the more elongate and slender body form of these taxa, even as compared with the one other endemic species from that lake. To judge from the skull proportions of *L. rhachirhinchus*, this species had a body form more like that of *L. microlepis* or *L. mariae* than that of *L. niloticus* or its close relatives.

Urostylar vertebrae. The few (4) specimens of fused first ural and first preural centra available show no outstanding characters; in two the fourth hypural is still attached.

OTHER SKELETAL REMAINS including fin rays and supporting bones. Little of the pectoral girdle and its associated bones is preserved. There is part of a scapula (the articular surface) and a fragment of bone thought to be part of an extrascapula. Neither bone shows any specifically diagnostic features.

Nothing can be identified as coming from the pelvic girdle, except for the proximal end of a large pelvic spine. However, since this specimen is from Sinda-Mohari Point 6 (see p. 115) it is not necessarily from *L. rhachirhinchus*. Certainly it provides no features to distinguish it from a spine of *L. niloticus*.

The collection does contain a large number of percoid dorsal and anal fin spines, some complete but the majority damaged. Since most of the specimens are from Sinda-Mohari Point 10 it is very probable that they were derived from L. *rhachirhinchus*, although the possibility of at least the smaller specimens coming from a large cichlid fish (e.g. *Sarotherodon*) cannot be set aside.

RELATIONSHIPS of *Lates rhachirhinchus*. As yet there is no published account of any detailed arguments supporting a postulated phyletic arrangement of species within the genus *Lates*, nor of the relationships between these taxa and *Luciolates stappersi*. Sorbini (1973) reviewed the relationship between *Lates* and the Eocene taxon *Eolates*, and also considered the status of certain extinct *Lates* species. But, because Sorbini has made only a moderately detailed study of one extant *Lates* species and did not consider *Luciolates*, his conclusions must be viewed with certain reservations.

One of us (P. H. G.) is currently investigating the interrelationships of *Lates* species and their relationship with *Luciolates*; our assessment of the phylogenetic position of *L. rhachirhinchus* is to a large extent based on provisional conclusions stemming from that study.

There appear to be two major lineages within Lates. One line comprises the endemic species of Lake Tanganyika (L. angustifrons, L. mariae, L. microlepis and Luciolates stappersi). The other line comprises L. calcarifer, L. niloticus, L. macroph-thalmus and the extinct species L. fajumensis from Egypt. (For details of L. fajumensis see Weiler 1929.) The Tanganyikan lineage, including Luciolates whose generic status is under review, must be considered the derived (apomorph) sister group of the L. calcarifer-niloticus assemblage.

Lates rhachirhinchus has many derived characters that are not present in either of the lineages noted above – for example the vomerine spine, the poorly developed post-temporal fossa, and the various unique features in its jaw and associated bones. Indeed, we can find no derived features that are shared with the *L. calcariferniloticus* line. However, *L. rhachirhinchus* does share at least one apomorph feature with all members of the Tanganyika lineage, namely narrowing of the skull, and another, marked morphological differentiation between anterior and posterior caudal centra (p. 96), with two members of that line. All members of the Tanganyika lineage, including those species without a clear-cut differentiation in centrum shape, show apomorph features not found in *L. rhachirhinchus* and thus are more closely related *inter se* than is any one species with *L. rhachirhinchus*. Nevertheless, the affinities of the latter species seem, on the basis of skull form and vertebral characteristics, to be with the Tanganyika species rather than with *L. niloticus* and its immediate relatives.

It still remains to ask whether these resemblances are manifestations of convergence rather than an expression of close phyletic affinity, a question rendered more pertinent by the suite of unique apomorph characters found in *L. rhachirhinchus*. For example, does *L. rhachirhinchus* represent a taxon derived from a *L. niloticus*like ancestor which evolved rapidly in a local and isolated water body while its sister species continued to exist, unchanged morphologically, in neighbouring waters? The evolution during the Pleistocene of a distinct species (*L. macrophthalmus*) in Lake Albert, and of a so-called subspecies (*L. niloticus longispinis*) in Lake Rudolf, shows that isolated populations of *L. niloticus*-like species do respond to this type of evolutionary situation, albeit in these examples with less morphological divergence than is seen in *L. rhachirhinchus*. If such should have been the evolutionary history of *L. rhachirhinchus*, then the apomorph characters shared with the Tanganyika lineage would be of no value as indicators of its true phylogeny.

On the other hand, the specializations it has in common with the Tanganyika lineage could reflect a relationship with the ancestral species of that flock, assuming that the lineage had branched off from the *L. niloticus* group before it entered the Lake Tanganyika basin.

For the moment there is no evidence which will enable us to test either hypothesis, and so phyletically *L. rhachirhinchus* must be kept *incertae sedis*. One conclusion is, however, definite. During the early Quaternary there existed in eastern Africa a *Lates* species showing far greater morphological differentiation than either *L. calcarifer* or *L. niloticus*, the two most generalized extant members of the genus.

The temporal and geographical distribution of L. *rhachirhinchus* may well have been restricted. A species of *Lates* is abundantly represented in deposits of Lower Pleistocene age at Kaiso, Uganda (White 1926), some 100 km to the north-east of Sinda-Mohari, and in Lower to Upper Pleistocene deposits at and near Ishango, some 150 km to the south-west (Greenwood 1959). The taxon represented by these bones is certainly not *L. rhachirhinchus*, nor are there indications of its being closely related to that species. Indeed, as far as can be told from the bones preserved, these Kaiso and Ishango fishes are indistinguishable from *L. niloticus*.

Possibly the latest record is from Lower Pleistocene (Villafranchian) beds at Sinda-Mohari, Point 6 (p. 115). Geographically, the centre of L. *rhachirhinchus* distribution is in the Sinda-Mohari area, with only one possible record from Nyamavi (p. 116) outside it.

Superorder OSTARIOPHYSI Order CYPRINIFORMES Family ? CHARACIDAE

The most outstanding fish remains in the entire collection are fifty-seven large and peculiarly shaped teeth derived from an undescribed characoid fish. Most of this material comes from outcrops on the left bank of the Sinda river, but a few specimens are from other sites in the Sinda-Mohari area, and one is from the Karugamania beds of Lake Albert (map, Gautier 1970 : fig. 1).

That these teeth are from a characoid fish is clearly demonstrated by comparative morphological and histological studies. Great difficulty was encountered, however, when we attempted to determine the family in which the fish should be placed. None of the teeth corresponds exactly with teeth from any extant African characoid (i.e. members of the families Characidae, Hepsetidae, Distichodontidae, Citharinidae or Ichthyboridae). A closer correspondence exists between some of these teeth and those found in certain neotropical Characidae of the subfamily Serrasalminae. The teeth that do not resemble Serrasalmine types have a peculiar cusp pattern otherwise known only from an extinct taxon currently referred to the genus *Alestes* (Greenwood 1972).

It is for these reasons that we are uncertain about the familial status of the taxon which these teeth represent. We have therefore placed it tentatively in the Characidae. A more definite conclusion might have been reached had there been any bones associated with the teeth. No characoid skeletal remains whatsoever are recorded from any of the sites we have studied. This absence is surprising and quite inexplicable. Most other fish taxa from these deposits are well represented by a variety of bones, and it is difficult to believe that the jaws associated with the characoid teeth were in any way more delicate or less likely to be fossilized than were these other bones.

Genus SINDACHARAX nov.

1972 Alestes (part) : Greenwood, 506-511 (A. deserti, see p. 104 below).

DIAGNOSIS: Characoid fishes with a markedly heterodont dentition, in which some teeth are basically unicuspid (Fig. 23A), some very weakly tricuspid (Fig. 21A), and some are multicuspid with one major cusp and two or three serially arranged ridges of cuspules (Fig. 22B), a crown pattern not found in any extant characoid taxon (see below, p. 105).

TYPE SPECIES : S. lepersonnei sp. nov.

Sindacharax lepersonnei sp. nov.

DIAGNOSIS: Differs from the only other known species in the genus (see p. 105) in the shape and proportions of its teeth, and in having the majority of cusp ridges on the premaxillary inner teeth composed of interconnected cuspules and not continuous ridges (cf. Figs 22-24 with Greenwood 1972 : pl. 1, figs 2-8).

ETYMOLOGY. The species is named in honour of Dr Jacques Lepersonne of the Musée Royal de l'Afrique Centrale, Tervuren, as an appreciation of his contributions to African palaeontology and geology.

HOLOTYPE: A presumed premaxillary inner tooth (type I) from sites nos 145 and 156 (surface finds derived from basal Sinda Beds) on the left bank of the Sinda river, Zaire (Fig. 22B, specimen c). RG.17.599.

PARATYPES : Thirty-five other teeth from the same locality. RG.17.600.

AGE AND LOCALITY. The majority of teeth are from the Sinda-Mohari area (Gautier 1970 : fig. 1), and from the basal Sinda beds of presumed earlier Pleistocene (Lower Villafranchian) or uppermost Pliocene age (see p. 74 for further discussion on this dating). Three teeth are, however, from Miocene beds on the right bank of the Mohari river (outcrop L98), and another is from the Lower Miocene beds of Karugamania (c 12 km west of Lake Albert and some 20 km north of the Semliki delta region; Gautier 1970 : fig. 1).



FIG. 22. Sindacharax lepersonnei. Premaxillary teeth. A. Outer row teeth ; from left to right : two teeth in occlusal view, one in lateral view (paratypes). B. Inner row teeth in occlusal view, and arranged as teeth from the left premaxilla (i.e. medial tooth on left of row, and labial face of teeth towards top of page). From left to right the teeth are : (a) Type II, (b) Type III, and (c) Type I. C. The same teeth but viewed from an anterior and lower position so as to give an oblique quartering view of their crowns. The lingual aspect of the teeth is towards the bottom left-hand corner of the page. (Paratype lots RG.17.599 and 17.600.)

DESCRIPTION. This is based on the 36 type specimens, although details were checked against the 21 specimens of the hypodigm (see pp. 107-115).

Without corresponding jaw bones it has proved difficult to establish from which jaw the various teeth were derived, and virtually impossible to tell precisely the position of a particular tooth in the tooth row of its jaw. Our identification of the jaw, and a tooth's position in that jaw, is based on the approximation of fossil tooth morphology to that of teeth in living *Colossoma* and *Alestes* species. It must be considered conjectural.

Upper jaw. Outer row (II specimens). Only one form of tooth is represented in the paratypical sample, or amongst non-typical material. At first sight the tooth appears to be unicuspid and the cusp triangular, with its lingual face slightly concave and sloping steeply to the base where it becomes a narrow, near horizontal shelf



FIG. 23. Sindacharax lepersonnei. Dentary teeth. A. Tooth from outer row, in (i) occlusal and (ii) lateral views. B. Inner tooth in (i) occlusal and (ii) lateral views. (Paratype lot RG.17.600.)

(Fig. 22A). The cutting edge of the cusp, formed where the convex labial and concave lingual faces meet, has a clearly defined, broadly U-shaped outline, with the base of the U directed labially. On each side, at its junction with the base, there is a small, low cuspule. Thus, the tooth can be considered as a tricuspid in which the median cusp is disproportionately enlarged.

The base of the tooth is almost circular, with the bone of attachment plicate and deeply indented on each side at the point where the cutting edge meets the basal shelf. The longest horizontal axis of the occlusal surface measures, in the II specimens, $8 \cdot 0$ (frequency 3), $9 \cdot 0$, $10 \cdot 0$, $11 \cdot 0$ (f2), $11 \cdot 5$, $12 \cdot 0$ and $13 \cdot 0$ (f2) mm.

In their overall morphology these teeth closely resemble those in the anterior half of the outer premaxillary row of *Colossoma* species; there is little similarity with outer premaxillary teeth in any *Alestes* species.

Inner teeth. Three different types of teeth are thought to be from the inner row of the premaxilla. In type I the occlusal outline is a distorted ovoid. On one margin there is an epicentrically placed cusp flanked on one side by a single low cusp and by three low cusps on the other (Fig. 22B, C); the entire row of five cusps is slightly curved. There is a second row of two, or more often three, cusps, also low and arranged in a gently curving arc that is a mirror image of the first row, which it meets. At least one cusp in this second row is noticeably elongate. The third row of cusps is more in the nature of an indented ridge than a series of discrete cuspules, although at the narrow end of the ovoid the cuspules are more distinctly separated. The curvature of this row parallels that of the second row. There are four teeth of this type, two from one side of the jaw and two from the other. The longest horizontal axis of each tooth measures $12\cdot0$, $13\cdot0$, c $14\cdot0$ and $15\cdot0$ mm respectively.

11

In type II teeth the occlusal outline is a distorted ovoid, the narrow end of which is thrown into a single high and conical cusp. One face of this cusp (the longest one) slopes more steeply than the others so that, in effect, its apex is situated somewhat eccentrically. A ridge of three low, blunt cusps, one more elongate and discrete than the others, is arranged in a gentle curve, the concave side of which faces the single major cusp (Fig. 22B, a). Beyond this cusp ridge, and at a lower level, is a curvilinear ridge of about five or six poorly demarcated cusps. It parallels the first ridge and forms the occlusal margin of the crown. There is one well-preserved tooth of this type, and one badly worn specimen. The longest horizontal axis of each tooth measures 12·0 and c 8·0 mm respectively.

Type III teeth have an almost circular occlusal outline. The crown is dominated by a distinct central cusp whose wide but compressed shoulders form a crest extending across almost the complete diameter of the crown. At each margin of the crest there is a low minor cusp forming part of a circlet of similar cuspules that encircles about three-quarters of the crown's margin (Fig. 22B, b). The whole occlusal surface slopes downwards towards the presumed lingual side of the tooth. It is at the lowest point of the crown that the circlet of cuspules is interrupted. The bone of attachment is flared away from the vertical axis of the tooth on this lower side. There are three type III teeth, whose longest horizontal axes measure 9.5, 9.0 and 5.5 mm respectively.

On the basis of tooth outline in *Alestes macrolepidotus* and *Colossoma bidens* we would suggest that teeth of type II are from the midline of the jaw (that is, the first tooth in the row of each premaxilla), those of type III are next in position and are followed by teeth of type I. On this reckoning, *S. lepersonnei* would have had at least six teeth in the inner row of the upper jaw.

Our reconstructed arrangement of premaxillary teeth in this species (Fig. 22B, C) would, therefore, give an outer row of stout, functionally unicuspid but morphologically tricuspid teeth and an inner row of at least six molariform teeth with complex crown patterns of three different types. The basic crown pattern of each type is a single cusp and from one to three rows of minor cuspules.

Lower jaw. Outer row. Two types of presumed outer dentary teeth are recognizable (Figs 23A and 24).



10mm

FIG. 24. Sindacharax lepersonnei. Dentary tooth from outer row, possibly the median tooth of this row (see text, p.103). (Paratype lot RG.17.600.)

In one (Fig. 23A) the outline of the occlusal surface is roughly cardiform, but without the median depression of a stylized heart. There is a single large, compressed and conical cusp whose peak lies at about the middle of the occlusal surface, but whose compressed shoulders extend to the margins. These shoulders are of unequal length. That on the side nearest the narrow end of the tooth is longer and slopes gently and gradually to merge with the crown's margin. The shorter shoulder at first slopes gently but then descends abruptly before merging with the margin. Both shoulders have, near their marginal extensions, a slight broadening of the cutting edge so that there is the semblance of a minor cuspule at that point. In other words, these teeth, like their counterparts in the upper jaw, are tricuspid. The presumed labial aspect of the crown is deeper than its lingual face, and there is a much deeper bone of attachment on that side as well, a condition common in the outer dentary teeth of several characoid species. There are six teeth of this type ; their longest horizontal axes are : $12 \cdot 0$ (f4) and $13 \cdot 0$ (f2) mm.

The second tooth type (Fig. 24) is represented by a single example (longest horizontal axis, $11 \cdot 0$ mm). It is basically similar to the other type of tooth, but has one face depressed into a broad and gentle concavity which distorts the cardiform outline characteristic of these teeth.

The position in the jaw cannot be established with any certainty for either tooth type. Since the outline of the first type (above) is not indented at any point it is less likely to be the medial tooth of the row. We argue thus because, in living characoids with an *Alestes* or *Colossoma* type of dentition, the median tooth is invariably recessed to accommodate the anterior face of the inner tooth. However, the second type of fossil tooth does have a very slight indentation on one aspect, and thus it may be the median tooth.

In their overall appearance and in their cusp pattern these teeth (and especially the second type) fairly closely resemble the antero-lateral outer row teeth from the dentary of C. bidens. Compared with the equivalent teeth in Alestes species, those of S. lepersonnei show a great reduction in cuspidation but have similarities in their outline shape and in the concave occlusal surface, a feature shared with the teeth of C. bidens.

Inner teeth. The basal outline of the teeth, of which only one type is recorded, is subcircular to oval. There is one large cusp with a well-defined cutting edge extending across the width of the base at an angle to its presumed lingual and labial margins (Fig. 23B). The posterior (i.e. lingual) aspect of the cusp is concave in lateral view, and the anterior face equally convex, so that the tip of the cusp is noticeably recurved. On the lingual aspect there is a narrow horizontal shelf that merges insensibly with the vertical face of the cusp.

Judged on the angle at which the cusp is orientated (see above, also Fig. 23B), left and right teeth are both represented in our sample. Also, since there is but one type of tooth referrable to the inner row, we conclude that there is only one inner tooth in each dentary.

The bone of attachment is deeply plicate, as it is in all other teeth of this species. The ventral plane of the tooth is, however, distinctly concave and is more markedly so on one side than the other. There are nine presumed inner dentary teeth divisible into two groups, of five and four teeth each, on the basis of cusp orientation. The longest horizontal axis measures $8 \cdot 0$, $8 \cdot 5$, $9 \cdot 0$ (f3), $10 \cdot 0$, $11 \cdot 0$ (f2) and $11 \cdot 5$ mm.

In their gross morphology these teeth differ only slightly from their counterparts in *Alestes macrolepidotus*, although in that species the bone of attachment is much deeper and the cusp is rather less compressed. There is far less similarity with the inner teeth of the serrasalmines *Myletes* and *Colossoma*.

According to our identification of these various lower jaw teeth, *S. lepersonnei* would have had an outer row of stout, essentially unicuspid teeth with well-defined shearing edges and a small, horizontal surface behind the cusp. The first (or medial) tooth may have had this surface indented to receive the basal crown part of an inner tooth. The number of outer teeth cannot be determined, and there is little variation in the morphology of the outer teeth available to us. From the ventral outline of the bone of attachment we conclude that the teeth were attached to the dentary in exactly the same manner as are the outer teeth in extant characoids. Thus, each tooth would have a deep labial aspect and a shallow lingual one.

The inner dentary tooth row probably consisted of a single pair of stout unicuspids, one tooth on each ramus, differing little in their shape from those of many extant characoids.

Size. The teeth on which the taxon S. lepersonnei is based are large. Indeed, we have been unable to examine any extant serrasalmine or alestine characoid with teeth of a comparable size. In the largest C. bidens available to us, a now incomplete skeleton from the BM(NH) collections, the maximum length of the longest horizontal axis of the largest premaxillary outer tooth is $6 \cdot 0 \text{ mm}$ (cf. 13.0 mm in Sindacharax), of the largest premaxillary inner tooth $8 \cdot 0 \text{ mm}$ (cf. 15.0 mm), of the largest dentary outer tooth $8 \cdot 0 \text{ mm}$ (cf. 11.5 mm). The C. bidens skull measures 10.7 cm from the premaxillary symphysis to the basioccipital facet.

RELATIONSHIPS of *Sindacharax*, and the generic status of *Alestes deserti* Greenwood 1972. Taken in their entirety, the known teeth of *S. lepersonnei* do not resemble those of any extant species of African characoid. In many respects the closest resemblance, except for the inner premaxillary teeth, is with the dentition in certain New World serrasalmines, especially those of the genus *Colossoma*.

The only extinct African characoid for which dental details are available is A. deserti Greenwood, a species from the Pliocene of Wadi Natrun, Egypt.* (Fossil teeth of *Hydrocynus* are, of course, irrelevant to this discussion, as is the Eocene characoid from France whose teeth are certainly more like those of extant Alestes than those of either A. deserti or S. lepersonnei: Cappetta, Russell & Braillon 1972; also personal observations.)

^{*} Since this paper was completed, three further specimens of A. deserti teeth have come to light; all are from Kaiso, Lake Albert. Thus, not only is the range of this species extended geographically, but also temporally, into the range of *S. lepersonnei*. One of the new specimens, a third inner premaxillary tooth, is from Kaiso Village; the other two, a first inner premaxillary tooth (BM(NH) reg. no. P49205), and a worn tooth, possibly a third outer row dentary (P49206), are recorded merely as being from Kaiso, collected by Capt. C. R. S. Pitman, 1929.

The teeth of *A. deserti* depart quite markedly from those in all extant species of *Alestes*, and the Eocene species from France, particularly in having ridge-like cusps on teeth from the inner premaxillary series. In this respect the teeth of *A. deserti* resemble their counterparts in *S. lepersonnei*. There are also certain resemblances between some outer dentary teeth as well. On the other hand, no detailed similarities between inner premaxillary teeth in the two taxa could be found, and there are some differences in their outer premaxillary and outer dentary teeth. But, despite these dissimilarities and some similarity with the dentition of *A. macrolepidotus* (Greenwood 1972), the presence of cusp ridges across the inner premaxillary teeth in only *A. deserti* and *S. lepersonnei* is a characteristic that cannot be dismissed lightly.

As far as we can determine, the development of cusp ridges should be looked upon as a derived character state, and one coordinate with the cusp patterns found in extant *Alestes* species (see Greenwood 1972, for further discussion). This in turn leads us to consider whether or not *A. deserti* should be removed from the genus *Alestes* and treated as a taxon cognate with *Sindacharax*, and whether the two taxa should be placed in a suprageneric category distinct from the alestines.

The dental similarities of S. lepersonnei and A. deserti have been described, and the differences noted. What is perhaps significant here is the fact that in one of the differences, in the first dentary tooth, A. deserti resembles Colossoma bidens, and that the other may be fallacious and due to a misidentification of the position occupied by the tooth concerned in A. deserti, or for that matter in S. lepersonnei. We say this because the presumed outer premaxillary tooth in A. deserti closely resembles the presumed inner premaxillary tooth of type III in S. lepersonnei. These, the major dental differences separating S. lepersonnei and A. deserti more closely with the genus Alestes, and that both have features that are reflected in the dentition of Sindacharax (compare Figs 22-24 with Greenwood 1972 : plate I, figs 2-8).

Taking all these factors into account we therefore conclude that the several shared dental specializations found in *S. lepersonnei* and *A. deserti* indicate a closer relationship between the species than exists between *A. deserti* and any other species of the genus *Alestes. Alestes deserti* is accordingly now placed in the genus *Sinda-charax*.

Any possible relationship between *Sindacharax* and certain elements, for example *Myletes* and *Colossoma*, of the serrasalmine lineage (now confined to the New World) is, of necessity, based on close resemblances in the outer teeth of these taxa (see pp. 100 and 102). The widespread occurrence of multicuspid outer teeth in the Characoidei suggests that the reduced cuspidation seen in serrasalmines and in *Sindacharax* is a derived condition, and therefore one possibly indicative of relationship between them. This assumption should not be construed as contradicting Roberts' (1967) thesis that unicuspid teeth are primitive in characoids. The teeth in *Sindacharax* and the serrasalmines are either basically tricuspid (with the median cusp hypertrophied) or of a unicuspid type that is no more like the presumed primitive kind (e.g. as in *Hoplias* or *Salminus*) than are the unicuspids of *Hydrocynus* (Roberts 1967).

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Our thoughts on the problem of relationships between the serrasalmines and *Sindacharax* lead us to wonder whether perhaps *S. lepersonnei* and *S. deserti* are the last traces of an Old World serrasalmine lineage, a line that deviated from its New World relatives in having transversely multicuspid inner premaxillary teeth.

III. ANNOTATED LIST OF THE FISH REMAINS

The two new taxa from this collection, *Lates rhachirhinchus* (Centropomidae) and *Sindacharax lepersonnei* (? Characidae) are fully described on pp. 74–98 and 99–104 respectively. In this part of the paper only the number and kinds of skeletal parts from these two species are listed for any site.

Other fish remains (catfishes, a lungfish, possibly a cichlid and a mormyroid) are, in contrast with the *Lates* specimens, rather poorly represented in terms of both the number and variety of bones preserved. Geographically, however, most of these taxa are widely distributed within the area under consideration.

Identifying fishes from such fragmentary remains as these is not a simple task, and often cannot be carried with any confidence beyond the generic level. An important factor here is the ironical one that we generally had available a greater number of fossil specimens than of skeletal preparations from living species. Thus it is difficult to determine the range of interspecific variability for the extant species, and therefore to evaluate the significance of apparent morphological differences between them and the fossils. It follows, too, that we had no yardstick against which to measure possible intraspecific or intrapopulational variability amongst the fossils.

Much of the fossil catfish material consists of damaged fin spines. When identifying these we have used characters of ornamentation (ridges, tubercles, serrations, etc.) on the spine itself, and in the case of pectoral spines the morphology of the complexly folded articulatory proximal end. To a lesser degree, the proximal end of the dorsal fin spine also yields diagnostic characters. Among living catfishes these different features seem to be reliable for identification at the generic level, and in the case of mochokid pectoral spines even at the species-group level. The vertebral column, excluding the rarely preserved Weberian apparatus, yields fewer characters, and these are only reliable at a familial or higher level. The few syncranial bones preserved proved to be of little diagnostic value because of the damage they had sustained.

In the list that follows, the sites are grouped into three geographical subregions, viz. the Sinda-Mohari area (area 3 in Gautier's (1970) map, fig. 1), the Lake Albert and Nyamavi areas (1 and 2 in Gautier's map), and the Lake Edward and Upper Semliki areas (5 and 6 in Gautier's map). The entire region covered is thus essentially that lying between the northern end of Lake Edward and the south-western end of Lake Albert.

Sinda-Mohari Area

SINDA-MOHARI, POINT 15. Kabuga Formation (Lower Miocene).

Protopterus sp. Part of a left mandibular tooth plate and its associated cartilage is the sole representative specimen of this genus. In its morphology, the fossil compares closely with the equivalent tooth plate in living *P. aethiopicus*.

Auchenoglanis sp. A damaged proximal end from a left pectoral fin spine is referred to this genus with certainty, and a fragment of neurocranial bone is thought to be from an Auchenoglanis.

Clarotes sp. A fragment from the anterior part of the left frontal agrees in almost all details with that region of the bone in extant *C. niloticus*.

? Bagridae or Clariidae. A piece of centrum, showing the typical antero-posterior compression seen in the first free centrum of *Bagrus*, and in the anterior abdominal centra of clariid fishes, cannot be identified further.

Part of a fin spine (compressed and with serrations on one face only) may be a fragment of pectoral spine from a *Synodontis*. Its linear and somewhat sinuous ornamentation is like that in extant *Synodontis*, as is its generally compressed form.

Unidentifiable catfishes. Four fragments of fin spines (one definitely a dorsal spine) cannot be identified to family.

Lates, probably L. rhachirhinchus. Centropomids are not well represented, there being only one specimen of a first vertebra, one of a posterior abdominal vertebra and a gill raker. The morphology of the first vertebra is like that of L. rhachirhinchus (see p. 91).

OUTCROP NO. L98, RG2527-497. Right bank of the Mohari river. Mohari Beds (Lower Miocene).

Lates cf. L. rhachirhinchus. Two first vertebrae and a third vertebra all show features of these elements in L. rhachirhinchus, see p. 91. But since the specimens are damaged, the identification is considered to be a tentative one.

Auchenoglanis sp. The proximal, that is articular, end and about the proximal half of a dorsal fin spine is referred to this genus, as is another specimen (more incomplete) of a dorsal spine (the articular end and spine base only).

Synodontis sp. The articular head and the base of a pectoral spine (left) is referred to this genus.

Unidentifiable catfishes. Seven fragments of spines (from both dorsal and pectoral fins) are definitely from catfishes but cannot be identified further.

Sindacharax lepersonnei. The 4 teeth (I outer premaxillary, I outer and 2 inner dentary) from this site constitute one of the earliest records for *S. lepersonnei*. As far as we can determine, there are no morphological differences between these teeth and those from later (earlier Pleistocene) deposits; see pp. IIO-II4. The tooth from the outer row of the dentary is of the type I tooth described on p. IO3.

ONGOLIBA BONE BEDS. (Material collected by de Heinzelin from Ongoliba in 1957 is included here.) Ridge 1, basal Sinda Beds (? earlier Pleistocene ; see p. 74).

Synodontis sp. One almost complete but slightly damaged dorsal fin spine is definitely referable to this genus, while II fragments of dorsal and pectoral fin spines are probably also referable to this taxon.

Siluriformes, indeterminable. One damaged centrum (30 mm wide), from the anterior abdominal part of the vertebral column, resembles comparable elements in extant members of the Bagridae and could well be from a *Bagrus* species.

Lates rhachirhinchus is well represented by 117 specimens including 13 from the skull, 9 jaw bones and 9 specimens of bones from the suspensorium. The vertebral column is represented by 9 first vertebrae, 13 third, 15 (and possibly 2 others) of the fourth or fifth vertebra, 2 sixth, 2 seventh and 44 posterior abdominal and caudal vertebra. Much of the syncranial material is included amongst the paratypical specimens (see p. 74).

Some indication of the size of the fishes preserved may be gained from the following measurements :

- First vertebrae : breadth of anterior face in largest specimen c 37 mm, and in the smallest 14 o mm.
- Third vertebrae : breadth of anterior face in largest specimen 51.0 mm, and in the smallest 20.0 mm.
- Fourth-fifth vertebrae : breadth of anterior face in largest specimen 55.0 mm, and in the smallest 16.0 mm.

The caudal and posterior abdominal vertebrae are from fishes in a similar size range.

SINDA-MOHARI, POINT I, RIDGE I. Derived blocks and fossils from the Ongoliba Bone Bed (? earlier Pleistocene ; see p. 74).

? Synodontis sp. Three pieces of fin spine are almost certainly referable to this genus.

Clariidae. A fragment of left frontal, comprising half of the fontanelle, part of the anterior interfrontal suture, a little of the bone lateral to the fontanelle, and the anterior angle of the bone, is typically clariid in its morphology, and does not resemble the frontal in any other family of extant African catfishes. This specimen is one of the few near-definite remains of a clariid fish found amongst the material from Sinda-Mohari, although some of the small neurocranial fragments from these deposits could be from fishes of this family. It is surprising that no pectoral fin spines nor, for that matter, any other skull fragments were recovered (but see p. 112).

Lates rhachirhinchus is well represented by 6 neurocranial fragments, 4 pieces of dentary, I premaxilla, 6 bones from the suspensorium, I gill raker and a total of 75 vertebrae (5 first vertebrae, I0 third, 7 fourth or fifth vertebrae, 2 ? sixth and I ? seventh vertebrae, and 50 posterior abdominal and caudal elements).

As an indication of the size range of L. *rhachirhinchus* represented at this site the following measurements are relevant :

First vertebrae : breadth of anterior face in the largest specimen $23 \cdot 0$ mm ; in the smallest $6 \cdot 8$ mm.

Sixth vertebrae : breadth of anterior face 52.0 mm, length of centrum 36.0 mm.

The caudal vertebrae indicate that smaller fishes were also present.

SINDA-MOHARI, POINT 2. Mear Ongoliba; as for Point I, see above (Ongoliba Bone Bed; ? earlier Pleistocene).

Clarotes sp. Two fragments of pectoral spines, both right, are referred to this genus, and closely resemble those of the *Clarotes* species from Point 10 (see p. 000). Some possible *Clarotes* vertebrae are mentioned below.

Auchenoglanis sp. The genus is represented by the proximal ends of 2 pectoral spines (I left and I right from fishes of different sizes), and by a fragment from the distal end of a pectoral spine. In addition, the proximal end of another spine is tentatively referred to this taxon. The morphology of the articular head of the spine in this specimen does differ from that in the others, as does the ornamentation visible on the spine itself. Nevertheless, its overall morphology is closer to that of an Auchenoglanis pectoral spine than to that of any other genus.

Synodontis sp. Nineteen pectoral spines (9 left, 10 right), mostly comprising the articular head and proximal part of the spine, are referred to Synodontis. Judged on the ornamentation of these spines, only one species is represented in this material; it appears to be identical with 'species A' from Point 10 (see p. 000). Eight smaller spine fragments should probably be referred to this genus, but no specific identification is possible.

Also identified as being derived from a *Synodontis* species are 17 dorsal fin spines. Like the pectoral spines, these are mostly damaged specimens comprising the proximal part of the spine and its anterior region. Thirteen of the spines have a serrated anterior margin, with the serrations distinct and prominent, and a smooth posterior face at least proximally. In these characteristics, the spines resemble those of 'species A' from Point 10. The remaining 4 spines have a sharp, keel-like anterior margin and serrations on the posterior face, thus resembling specimens referred to 'species B' from Point 10 (see p. 000 below).

Two small fragments are probably from the list-1

• of a dorsal spine, and 95 is impossible to tell from

Reletin of the British Museum (Natural History) Geology 26 (3).

ones cannot be identified wo taxa are represented, *odontis*. Five vertebrae

The missing page references on page 109 are to page 111.

in certain catfishes) would seem to be from a bagrid, and are very tentatively identified as being from a species of *Clarotes*.

Lates rhachirhinchus. Specimens from this site cover a fairly wide spectrum of skeletal parts and a wide size range of individuals. Vertebrae are particularly well represented (313 specimens).

The skull is represented by 3 vomers and 8 basioccipitals, the jaws and suspensorium by 2 articulars, I quadrate, I dentary and 6 premaxillae, not including some fragments from the dentigerous arm of that bone, and the branchial skeleton by 16 gill rakers. One fragment can definitely be identified as part of a scapula, and another is tentatively identified as being part of an extrascapula. One large fin spine is provisionally referred to this species because of its size.

The vertebrae are identified as follows :

First: 24 specimens. Breadth of anterior face in largest specimen 60 mm, and in the smallest 8.0 mm.

Siluriformes, indeterminable. One damaged centrum (30 mm wide), from the anterior abdominal part of the vertebral column, resembles comparable elements in extant members of the Bagridae and could well be from a *Bagrus* species.

Lates rhachirhinchus is well represented by 117 specimens including 13 from the skull, 9 jaw bones and 9 specimens of bones from the suspensorium. The vertebral column is represented by 9 first vertebrae, 13 third, 15 (and possibly 2 others) of the fourth or fifth vertebra, 2 sixth, 2 seventh and 44 posterior abdominal and caudal vertebra. Much of the syncranial material is included amongst the paratypical specimens (see p. 74).

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The caudal and posterior abdominal vertebrae are from fishes in a similar size range.

SINDA-MOHARI, POINT I, RIDGE I. Derived blocks and fossils from the Ongoliba Bone Bed (? earlier Pleistocene ; see p. 74).

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First vertebrae : breadth of anterior face in the largest specimen 23.0 mm; in the smallest 6.8 mm.

Sixth vertebrae : breadth of anterior face 52.0 mm, length of centrum 36.0 mm.

The caudal vertebrae indicate that smaller fishes were also present.

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Auchenoglanis sp. The genus is represented by the proximal ends of 2 pectoral spines (\mathbf{I} left and \mathbf{I} right from fishes of different sizes), and by a fragment from the distal end of a pectoral spine. In addition, the proximal end of another spine is tentatively referred to this taxon. The morphology of the articular head of the spine in this specimen does differ from that in the others, as does the ornamentation visible on the spine itself. Nevertheless, its overall morphology is closer to that of an Auchenoglanis pectoral spine than to that of any other genus.

Synodontis sp. Nineteen pectoral spine that to that of any other gends. Synodontis sp. Nineteen pectoral spines (9 left, 10 right), mostly comprising the articular head and proximal part of the spine, are referred to Synodontis. Judged on the ornamentation of these spines, only one species is represented in this material; it appears to be identical with 'species A' from Point 10 (see p. 000). Eight smaller spine fragments should probably be referred to this genus, but no specific identification is possible.

Also identified as being derived from a *Synodontis* species are 17 dorsal fin spines. Like the pectoral spines, these are mostly damaged specimens comprising the proximal part of the spine and its anterior region. Thirteen of the spines have a serrated anterior margin, with the serrations distinct and prominent, and a smooth posterior face at least proximally. In these characteristics, the spines resemble those of 'species A' from Point 10. The remaining 4 spines have a sharp, keel-like anterior margin and serrations on the posterior face, thus resembling specimens referred to 'species B' from Point 10 (see p. 000 below).

Two small fragments are probably from the distal part of a dorsal spine, and 95 others are tentatively referred to *Synodontis*, although it is impossible to tell from which fin spine they are derived.

Unidentifiable catfishes. Four pieces of skull roofing bones cannot be identified further. Differences in the ornamentation suggest that two taxa are represented, and that one may be *Auchenoglanis* and the other *Synodontis*. Five vertebrae (2 of which show the antero-posterior compression typical of the first free vertebra in certain catfishes) would seem to be from a bagrid, and are very tentatively identified as being from a species of *Clarotes*.

Lates rhachirhinchus. Specimens from this site cover a fairly wide spectrum of skeletal parts and a wide size range of individuals. Vertebrae are particularly well represented (313 specimens).

The skull is represented by 3 vomers and 8 basioccipitals, the jaws and suspensorium by 2 articulars, I quadrate, I dentary and 6 premaxillae, not including some fragments from the dentigerous arm of that bone, and the branchial skeleton by 16 gill rakers. One fragment can definitely be identified as part of a scapula, and another is tentatively identified as being part of an extrascapula. One large fin spine is provisionally referred to this species because of its size.

The vertebrae are identified as follows :

First: 24 specimens. Breadth of anterior face in largest specimen 60 mm, and in the smallest 8.0 mm.

Third: 25 specimens. Breadth of anterior face in largest specimen 54 mm, and in the smallest 9.0 mm.

- Fourth or fifth : 24 specimens. Breadth of anterior face in the largest specimen 53 mm, and in the smallest 6 o mm.
- ? Sixth: 3 specimens. Breadth of anterior face in the largest specimen 50 mm, and in the smallest 13 mm.
- ? Seventh : 10 specimens. Breadth of anterior face in the largest specimen 45 mm, and in the smallest 8-0 mm.

Altogether there are 227 posterior abdominal and caudal centra of which 125 are classified as the elongate posterior caudal type. The measurements of the largest and smallest centra in the latter group (i.e. elongate type) are : breadth of anterior face 19 mm and 4 mm; length 23 mm and 8 mm; width 14 mm and 3 mm. Measurements of the former group are : breadth of anterior face 49 mm and 8 mm; length 40 mm and 8 mm; width 48 mm and 6 mm.

? Cichlidae. Four vertebrae are tentatively identified as being derived from cichlid fishes; from their size, it is thought that the fishes represented were in the size range of 30-35 cm standard length, that is, within the adult size range of several living *Sarotherodon* species. Two of the centra may be from third vertebrae because there appear to be the remains of the base of the stout apophysis which is developed from that centrum in present-day *Sarotherodon*; also the rib facet of these specimens resembles that on the third vertebra in extant *S. niloticus*. The two other centra are identified as those of caudal vertebrae.

SINDA-MOHARI, POINT 3. Western slope of Ridge 2; fossils derived from the Ongoliba Bone Bed (? earlier Pleistocene).

? Synodontis sp. A small piece of dorsal fin spine is probably from a member of this genus.

Lates rhachirhinchus. The species is rather poorly represented by a fragment of the angulo-articular, a vomerine tooth patch and 6 vertebrae. Specific identification is based partly on the shape of the angulo-articular (seep. 88) and partly on the morphology of the third, fourth or fifth and ? seventh vertebrae (see p. 92).

SINDA-MOHARI, POINT 4. Right bank of the eastern branch of the Kabuga valley; fossils collected on the slopes, which are derived from the basal Sinda Beds (Zone A; ? earlier Pleistocene).

? *Clarotes* sp. Three fragments of skull roofing bones are ornamented with densely arranged, high and bluntly conical tubercles, very similar in appearance to those of extant *Clarotes* species.

? Auchenoglanis. Again, our tentative identification is based on similarities between the ornamentation on the two fragments of skull bone and skull bones in living species.

Lates rhachirhinchus. The species is represented only by vertebrae, namely: a first vertebra, a third, a sixth and a caudal vertebra. All are from fishes of c 45 cm standard length. The morphology of the first and third vertebrae is characteristic of L. rhachirhinchus.

SINDA-MOHARI, POINT 5. Ridge I. On slope towards the Kabuga river; reworked material derived from the lowest Bone Beds and the Sinda Beds, Zone A (? earlier Pleistocene).

Lates rhachirhinchus. Although poorly represented at this site by I palatine and I first vertebra, the palatine bone is of considerable interest (see p. 85).

SINDA-MOHARI, POINT IO. Ridge I, northern part. Material from a profile 2.5 and 3.1 m above the interface between the Sinda Beds and the Mohari Formation (Ongoliba Bone Bed; ? earlier Pleistocene). In many respects, including the number of fish species represented, this is the most important site in the Sinda-Mohari area.

Sindacharax lepersonnei (see p. 99). This peculiar characoid is represented by 6 fairly well-preserved teeth (2 from the lower jaw and 4 from the premaxilla), and 3 fragments of teeth.

? *Clarotes* sp. No material is definitely assignable to this genus, but the following are tentatively identified as *Clarotes* remains :

- (i) A right angulo-articular.
- (ii) Three damaged dorsal fin spines, comprising the articular head and a little of the spine itself.
- (iii) Two fragments of dorsal fin spine, distal end.
- (iv) Four pieces of skull roofing bone identified on the basis of the ornamentation.
- (v) Three (2 left and 1 right) extremely damaged pectoral fin spines, comprising the articular head and part of the spine.

? Auchenoglanis. Like the Clarotes material, that referred to Auchenoglanis is only tentatively so assigned :

- (i) Two dorsal fin spines, comprising the articular head and the proximal part of the spine.
- (ii) Four (2 left and 2 right) pectoral spines (damaged), comprising the articular head and the proximal sixth to half of the spine.
- (iii) Three small fragments of skull roofing bones identified on the basis of their ornamentation.

? Bagridae. One anterior abdominal vertebra (width of centrum $c 2 \cdot I$ cm), and a specimen of the first free centrum posterior to the fused centra associated with the Weberian apparatus (width $c 2 \cdot 8$ cm), are thought to be from a bagrid fish. The first centrum closely resembles that in extant *Bagrus docmac*.

Synodontis spp. The genus is best represented by numerous fin spines, amongst which two types of ornamentation can be recognized, suggesting the presence of two species.

Twenty-five specimens of *pectoral spines* (10 left, 15 right), each comprising the articular head of the spine and, in most cases, part of the spine as well, have both the anterior and posterior faces serrated. The anterior serrations are conical and extend to the base of the spine. The posterior serrae are flattened and dagger-like, and extend, or almost extend, to the base of the spine. This ornamentation type

will be referred to as 'Species A' (see p. 109). In addition to this material there are three spines of 'Species A' lacking the articular head.

Eight pectoral spines (5 left, 3 right), fragmented like those described above, are referred to as 'Species B'. In these the serrae on the anterior face are smaller, finer and more closely spaced. Serrae on the posterior aspect of the spine are like those on the anterior face.

Thirty-two fragments from the proximal part of the pectoral spine are tentatively

referred to *Synodontis*, but cannot be assigned to a particular 'species'. The *first pungent dorsal fin spine* is also ser arable into two types. In 8 specimens, referred to as 'Species A', the posterior face is smooth, while the anterior face carries stout, subconical serrae. The second type ('Species B') is represented by a single specimen in which the anterior face of the spine is produced into a sharp ridge, and there are some serrations on the posterior face, beginning at a point about one-third along the length of the spine.

In addition to the specimens, 17 other and more fragmentary spines are ten-tatively referred to *Synodontis*, as are 180 small fragments mostly from pectoral spines but including some thought to be from dorsal spines.

Unidentifiable catfishes. Several hundred small pieces of fin spines, probably from bagrid and mochokid catfishes, cannot be identified more precisely.

Lates rhachirhinchus. By far the greatest number and anatomical variety of specimens are from this site. There are 41 specimens of neurocranial fragments, 7 specimens are from this site. There are 41 specimens of neurocranial fragments, 7 maxillae, 51 premaxillae, 93 fragments of dentary, 55 bones or fragments of bones from the palatoquadrate arch (including one palatine bone, see p. 85), a fragment of scapula, part of what is thought to be an epihyal, 65 gill rakers and 9 fragments probably from branchiostegal rays. In addition there are 38 first vertebrae, 35 third, 28 fourth or fifth, 4 ? sixth and 7 ? seventh vertebrae, together with 172 posterior abdominal and caudal vertebrae, 8 specimens of the fused first ural and first preural centra, some with remains of hypurals still present, and a single isolated hypural. The holotype of the species, a vomer, is from this site. The material examined is derived from a wide size range of individual fishes; the largest is estimated to have had a standard length of c. 150 cm, i.e. within the size range of extant L milotious L. niloticus.

SITE 59. Downstream of Mtoto ya Ongoliba (Kabuga river). Probably derived from Sinda Beds.

Protopterus sp. A fragment of mandibular tooth plate is the only specimen referable to this taxon.

2 Clariidae. A fragment of dentary (including part of the alveolar surface) most closely resembles that region of a clariid dentary slightly anterior to the hind end of its dentigerous surface, i.e. where the body of the bone begins to narrow. The pattern of the dentigerous surface suggests a dense felt of small teeth. A piece of skull roofing bone also is tentatively referred to this family. If our identifications are correct, these two specimens together with the frontal from Point I (p. 108) are the only clariid remains from the Sinda-Mohari region, a surprising state of affairs

since clariid remains are usually the commonest fossils in Quaternary African lake and river deposits.

? Bagridae. Part of a dentary is tentatively identified as coming from a bagrid fish. The alveolar surface indicates that there was a fine felt of closely packed and small teeth. Although the horizontal curvature of this bone is like that in extant *Bagrus* species, its ventral profile has the form of a broadly rounded ridge, not a sharp one as in *Bagrus*.

SURFACE FINDS NO. L145, RG2628-531.* Sinda river, probably derived from basal Sinda Beds.

Sindacharax lepersonnei. The species is represented by 4 teeth, viz. I from the outer premaxillary row, 2 from the outer and I from the inner row of dentary teeth.

SURFACE FINDS NO. L145, RG2638-531(B). Left bank of Sinda river, probably derived from basal Sinda Beds.

Lates cf. L. rhachirhinchus. The only Lates material from this site consists of vertebrae, viz. 4 first, 3 third, 4 fourth or fifth, 1? seventh and 10 posterior abdominal and caudal elements. Judged on the characteristics of the first, third and fourth or fifth centra, the species is probably L. rhachirhinchus.

SURFACE FINDS NOS L146 and 156, RG2448-531(C). Left bank of Sinda river, probably derived from basal Sinda Beds.

Sindacharax lepersonnei. The species is represented by a total of 4 teeth, viz. 2 outer premaxillary teeth (one merely an enamel cap and therefore probably a replacement tooth), I inner premaxillary tooth (probably median in position) and I tooth from the outer series of the dentary.

Lates sp. probably L. rhachirhinchus. Four first vertebrae and one specimen of the fused first preural and ural centra are from a Lates. Three of the first vertebrae show the typical characteristics of this element in L. rhachirhinchus, but the fourth specimen is much compressed antero-posteriorly, especially over its ventral half. In this respect, it differs from all species and specimens of Lates we have examined.

OUTCROP NO. L100, RG2546-498A. Right bank of Mohari river, base of Sinda Beds.

Lates sp. possibly L. rhachirhinchus. The one first vertebra from this site is damaged but shows characteristics of that element in L. rhachirhinchus (p. 91). The posterior abdominal centrum shows no diagnostic features, but the relatively elongate caudal centrum is like that in L. rhachirhinchus.

OUTCROPS NOS L145 and L156, RG2650-531(C). Surface finds, base of Sinda Beds.

? Bagridae. Four damaged centra with the typical cancellous pattern and the overall morphology of caudal vertebrae in the genus *Bagrus* are referred, tentatively, to this family.

Lates rhachirhinchus. Only vertebrae of this species are recorded, and comprise : 19 first, 10 third, 13 fourth or fifth, 1 ? sixth, 2 ? seventh and 165 posterior abdominal and caudal vertebrae.

* This and subsequent RG numbers are locality numbers and not specimen register numbers.

I 2

? Cichlidae. A damaged posterior abdominal vertebra closely resembles comparable elements in the extant species *Sarotherodon niloticus*, and is referred, tentatively, to this family.

OUTCROPS NOS 145 and 156, RG2651-531(C). Left bank of Sinda river, base of Sinda Beds, Zone A (? earlier Pleistocene).

Lates rhachirhinchus. The species is represented by 5 incomplete dentaries (3 left, 2 right). The toothed area and the large lateral line canal pores are typical of L. rhachirhinchus (see p. 88).

OUTCROPS NOS 145 and 156, RG2653-531(C). Left bank of Sinda river, base of Sinda Beds.

Sindacharax lepersonnei. This site has yielded the greatest number and variety of S. lepersonnei teeth, and is the source of all paratypical material (see list on p. 99).

OUTCROPS NOS 145 and 156, RG2659-531(C). Site details as above.

Clarotes sp. A left pectoral fin spine (comprising the articular head and part of the spine), 2 fragments from the distal end of pectoral spines and a dorsal fin spine (proximal end) are placed in this genus on the basis of their ornamentation and on the morphology of their proximal, articular surfaces.

Synodontis sp. Five dorsal fin spines (proximal end) and 13 damaged pectoral spines (7 left, 6 right comprising the articular heads and proximal part of the spine) are identified as being from *Synodontis*; 5 proximal fragments of pectoral spines and 58 fragments of fin spines (pectoral and dorsal) are tentatively referred to this genus.

OUTCROPS NOS 145 and 156, RG2661-531(C). Site details as above.

Sindacharax lepersonnei. Two teeth, a lower inner and an upper inner.

Synodontis sp. A damaged left pectoral spine (proximal end) and 8 fragments of pectoral spines are tentatively referred to this genus.

OUTCROPS NOS 145 and 156, RG2663-531(C). Site details as above.

Lates rhachirhinchus. The species is represented by three bones, viz. a basioccipital (depth of facet for first vertebra $14 \cdot 0$ mm), a large fragment of the left anguloarticular showing the typical morphology for this species (p. 98) and a left premaxilla, damaged but with the specific characteristics preserved. A fourth specimen is tentatively identified as part of a centropomid ceratohyal.

LOCALITY UNRECORDED, RG2668-531(C). No other data.

Synodontis sp. Two dorsal fin spines (proximal ends only), 2 pectoral fin spines (both left, consisting of the articular head and proximal part of the spine) and 3 fragments from the distal ends of pectoral spines are referred to this genus.

MBOVO OUTCROP NO. LIII, RG2572-511. Sinda Beds, Zone B (Lower Pleistocene, Villafranchian).

Lates sp. The only specimen of this genus is a fragment of frontal still deeply embedded in a matrix that has proved resistant to chemical cleaning. Although the bone is certainly from a centropomid fish, it is not possible to determine from which species of *Lates* it was derived. OUTCROP NO. L162, RG2680-545. Right bank of Sinda river, Sinda Beds, Zone B (Lower Pleistocene, Villafranchian).

Lates sp. No species-diagnostic characters are obtainable from the one posterior abdominal and the one caudal centrum preserved at this site.

SINDA-MOHARI, POINT 6. Right bank of the Sinda river near the Semliki scarp, Sinda Beds, Zone C (Lower Pleistocene and younger than beds of Zone B).

Clarotes sp. The articular head and approximately the basal third of a left pectoral spine agrees in all morphological details with that spine in extant *Clarotes*.

Unidentifiable catfish. Part of a fin spine, probably from the pectoral fin, is certainly from a siluriform fish, but cannot be identified further.

Lates cf. L. niloticus and L. rhachirhinchus. Centropomid material from this site is of particular interest because, whenever diagnostic features are preserved, some specimens show greater similarity with the extant L. niloticus than with L. rhachirhinchus, the characteristic and unique species of earlier deposits. However, other bones do exhibit features that suggest L. rhachirhinchus. For example, the well-preserved angulo-articular shows in lateral view a shallow articular facet, contrasting with the deep facet of L. rhachirhinchus, and a posterior margin that does not rise steeply or incline anteriorly as it does in L. rhachirhinchus. Furthermore, the lateral-line canal underlying this surface is of the short, L. niloticus type (see p. 88). The three incomplete (I left and 2 right) dentaries, on the other hand, have the relatively narrow dentigerous surface and the large lateral-line pores characteristic of L. rhachirhinchus. A fourth fragment of dentary is too incomplete to show any diagnostic features. The vertebrae are perhaps nearer the L. rhachirhinchus type than those of L. niloticus. An exceptional specimen is the only second vertebra recorded from the entire Sinda-Mohari area. It is virtually identical with its counterpart in L. niloticus; indeed, it is nearer that than the second vertebra of L. calcarifer. Vertebral specimens comprise I second, 2 third, I fourth or fifth, I ? seventh and 2 posterior abdominal or caudal centra. Other Lates bones are part of a premaxilla (the dentigerous arm and therefore of no diagnostic value) and a pelvic fin spine. The latter, which comprises only the articular region and a short segment of the spine itself, is from a very large fish : the vertical depth of the spine and its articular surfaces is at least 2 cm since part is missing. It is difficult to draw any definite conclusions from these few specimens. Perhaps both a L. niloticus-like species and L. rhachirhinchus were present, or these bones may be from a third taxon which combined features of both species.

Lake Albert and Nyamavi areas

KARUGAMANIA BEDS (Lower Miocene). Collected by J. de Heinzelin.

Sindacharax lepersonnei. This taxon is represented only by a damaged type I tooth from the inner premaxillary series (p. 101).

Unidentifiable catfishes. A fragment of a strong fin spine, serrated on one face, is thought to be derived from a catfish.

Lates sp. A fragment of vertebra (centrum) is undoubtedly from a *Lates* but no specific identification is possible.

KARUGAMANIA BEDS (Lower Miocene), RG2279-445.

Lates sp. (probably L. rhachirhinchus). Lates remains from this site comprise an incomplete basioccipital, 2 specimens of a fourth or fifth vertebra, 3 of a ? sixth vertebra and I caudal element. The morphology of these abdominal vertebrae (especially the fourth or fifth) is virtually identical with that of comparable elements in L. rhachirhinchus from other localities (see pp. 107–115), and differs markedly from that in L. niloticus (or L. niloticus-like fossils). The caudal vertebra provides no diagnostic features.

KARUGAMANIA BEDS (Lower Miocene), RG2282-445.

? Mochokidae. A small portion of a fin spine is thought to be derived from a mochokid catfish.

KARUGAMANIA BEDS (Lower Miocene), RG2316-446, outcrop no. L48.

? Catfish. A large caudal vertebra (width of centrum 21.0 mm, depth 22.0 mm) is probably derived from a bagrid catfish.

NYAMAVI AREA, RG2485-490, outcrop no. L81 (Upper Miocene or Lower Pliocene).

? Bagridae. Three centra (respectively 29.0, 26.0 and 25.0 mm wide), probably from posterior abdominal vertebrae, are possibly from a bagrid species, but cannot be identified more precisely.

Lates sp. or spp. With only vertebral material available, it is difficult to be certain about the specific identity of the Lates preserved at this site. The two specimens of the third vertebra could be from either a L. niloticus-like fish, or from L. rhachirhinchus. The single specimen of a first vertebra seems to combine features of L. rhachirhinchus and features not found in that species or in any other Lates species living or extinct. The nature and pattern of the central trabeculae, and the shape of the 'saddle' separating the exoccipital facets, are L. rhachirhinchus-like. The centrum is noticeably narrowed antero-posteriorly over its ventral half, a feature seen in a few other fossils from this region (see p. 91) but not in extant Lates. Finally, the shape of the exoccipital facets is unlike that in any extant or extinct species.

NYAMAVI, outcrop no. L68, RG2395-464/1. Upper Nyamavi Beds, member VI (Lower Pleistocene).

Clarotes sp. Five pectoral fin spines (I left and 4 right), each comprising the articular head and base of the spine, are referred to this genus on the basis of articular surface morphology. Nine fragments from the distal part of the spine are also identified as *Clarotes* on the basis of their ornamentation. A large part of the fused vertebral mass associated with the Weberian apparatus shows, in some respects, certain similarity with that element in *Clarotes*. But in other ways it is unlike this structure in any living African catfish group. Because of the specimen's incompleteness, it seems unlikely that a more positive identification can be made.

? Auchenoglanis sp. Part of a right quadrate is referred to this genus because it has the characteristic articular surface of extant Auchenoglanis species.

? Synodontis sp. A damaged pungent dorsal fin spine (comprising the articular base and about the proximal third of the spine) has a smooth posterior face, and the anterior face ornamented with small, fine tubercles more or less fused into a narrow

ridge. In these respects it closely resembles one of the two types of *Synodontis* dorsal spine found in Lower Pleistocene beds of the Sinda-Mohari area (see p. 112). However, this specimen differs from the Sinda-Mohari species in having the small facets on its anterior face for the reduced first dorsal spine of a very different shape. Indeed, this shape was not encountered in any of the several extant *Synodontis* species we examined. For this reason our identification must be considered tentative.

NYAMAVI, RG2398-464/I. Upper Nyamavi Beds, member VI (Lower Pleistocene).

Clarotes sp. Five fragments of skull roofing bones are referred to this genus on the basis of their ornamentation.

NYAMAVI, outcrop no. L68, RG2406-464/1. Upper Nyamavi Beds, member VI (Lower Pleistocene).

Clarotes sp. A fragment of right operculum (upper third of the bone, including the articular facet) and 3 pieces of roofing bone are referred to this genus, the latter specimens with less certainty than the former.

NYAMAVI, outcrop no. L68, RG2398-464/1. Upper Nyamavi Beds, member VI (Lower Pleistocene).

Clarotes sp. Two articulars (I left and I right but from different individuals) and 2 fragmentary basioccipitals (width across facet 13.0 and 14.0 mm respectively) are referred to this genus with certainty. Another fragment appears to be part of a *Clarotes* post-temporal bone.

Lates sp. Seven poorly preserved centra (probably from caudal or posterior abdominal vertebrae) are the only Lates remains, and cannot be identified to species.

Lake Edward and Upper Semliki areas

LAKE EDWARD, 1000-1500 m east of Ishango, outcrop no. L273, RG2741-608. Lake Edward Beds (Lower Pleistocene, Villafranchian).

? Hyperopisus sp. (Fig. 25). Four low-crowned and generally molariform teeth are very tentatively referred to this or some closely allied and extinct genus. The teeth could be derived from the parasphenoid or basihyal tooth plates. In all specimens the crown shows signs of wear, and in some there is an eccentric pit like that produced when wear destroys a single cusp. The teeth are subcircular in outline and there is a variation in their relative crown length, some being flatter, others more domed. The maximum widths of the four teeth are $5\cdot0$, $7\cdot0$, $7\cdot5$ and $9\cdot0$ mm respectively; it is estimated that they are derived from a large fish of c 75-100 cm standard length. Very similar teeth, also tentatively identified as being from Hyperopisus, are recorded from the Lower Pleistocene deposits at Kanyatsi, east of Ishango (Greenwood 1959). More certainly identifiable Hyperopisus teeth come from the Pliocene beds of Wadi Natrun, Egypt (Greenwood 1972).

KANYATSI, 20-25 m above lake level, outcrop no. L275, RG2761-617. Lake Edward Beds (Lower Pleistocene, Villafranchian).

Lates sp. A fragment of centrum, probably from an anterior abdominal vertebra; no specific characters are preserved.

NYAKAVIA RAVINE, outcrop no. L283-285, RG2811-651. Lake Edward Beds (Lower Pleistocene, Villafranchian).

? Synodontis sp. A fragment from the proximal end of a dorsal fin spine, without the articular surfaces, is tentatively referred to this genus on the basis of its ornamentation (serrated posterior face; anterior face probably keeled).

Lates cf. L. niloticus, and also possibly L. rhachirhinchus. The genus is relatively well represented by a number of vertebral centra including some which show specifically diagnostic features.



FIG. 25. ? Hyperopisus sp. Isolated tooth (basihyoidal or parasphenoidal) in (top) occlusal and (bottom) lateral views.

First vertebra: 2 specimens (one damaged, the other in good condition). These bones resemble the centrum found in L. *niloticus* although one specimen has a shorter ventral than dorsal length, in that way resembling the first vertebra of L. *rhachirhinchus* (see p. 91). The other specimen is identical to this vertebra in extant L. *niloticus*.

Second vertebra : I specimen. Closely resembling that of L. niloticus.

Third vertebra : 2 specimens. It is not possible to be certain about the specific identity of these bones. A third and much smaller specimen is also tentatively identified as a third vertebra.

Fourth vertebra: I specimen. Although damaged, it is possible to say that this centrum closely resembles its counterpart in *L. niloticus*.

Fifth vertebra : 2 specimens (one entire, the other badly damaged) ; both are like that vertebra in *L. niloticus*.

Sixth vertebra : I specimen from a much smaller fish than those from which the other specimens were derived. It is identical to the sixth vertebra in *L. niloticus*.

Caudal and posterior abdominal vertebrae: A total of 31 centra, of which 10 show the characteristic elongation and narrow waisted condition typical for L. *rhachirhinchus*.

The remaining specimens cannot be identified to species.

RAVINE KIO, OUTCOP NO. L288, RG2830-658. Lake Edward Beds (Lower Pleistocene).

Lates sp. The single, damaged specimen of a third vertebra and 5 poorly preserved caudal (or posterior abdominal) centra cannot be further identified.

ISHANGO TERRACE, outcrop no. L298, RG2877-673. Upper Pleistocene.

Lates sp. One centrum, and the base of the right neural arch, of an abdominal vertebra, thought to be the eighth or ninth element in the series because of the size of its 'transverse process'. Specific identification is impossible.

ISHANGO TERRACE, outcrop no. L298, RG2883-673A. Upper Pleistocene.

Lates sp. cf. L. niloticus. A damaged vertebra, thought to be a fifth abdominal, compares closely with that vertebra in extant L. niloticus. There is also the centrum of a caudal vertebra; it cannot be specifically identified.

? Sarotherodon. Three centra (two posterior abdominal and a caudal) closely resemble those in a comparable-sized S. niloticus (Cichlidae). These bones are from a fish estimated to be about 30 cm standard length.

LAKE EDWARD, 1000-1500 m east of Ishango, outcrop no. L302, RG2893-677. Lake Edward Beds (Lower Pleistocene).

? Centropomidae. A fragment of a fin spine is referred to this family because of its large size, presumably too large to be derived from a member of the Cichlidae.

UPPER SEMLIKI, upstream from Senga, on the right bank; outcrop no. L315, RG2912-687. Lake Edward Beds (Lower Pleistocene).

Lates sp. One damaged centrum, probably caudal, still deeply embedded in an intractable matrix. Further identification is impossible.

UPPER SEMLIKI, RG2919-688. Site data and age as above.

Lates sp. The centrum of a third vertebra, for which no specific identification is possible.

UPPER SEMLIKI, 1000 m downstream from Senga ; outcrop no. L317, RG2925–690. Lake Edward Beds (Lower Pleistocene).

? Centropomidae. An almost complete dorsal fin spine is referred to this family because of its size.

UPPER SEMLIKI: Luamiti, outcrop no. L327-328, RG2944-693. Lake Edward Beds (Lower Pleistocene).

Clarotes sp. A fragment of a left pectoral fin spine, including the damaged articular head and the proximal third of the spine, is referred to *Clarotes* because of its ornamentation and the morphology of the articular head.

UPPER SEMLIKI, Mupanda, left bank, outcrop no. L328, RG2948-694. Lake Edward Beds (Lower Pleistocene).

Clarotes sp. A fragment from a right pectoral fin spine, including the articular head and the proximal part of the spine itself. The generic identification is based, principally, on the morphology of the articular head, but also on the ornamentation of the spine.

? Catfishes. Four fragments of vertebral centra from this site are thought to be from a catfish, but cannot be further identified.

IV. CONCLUSIONS

Generally it is impossible to identify fragmentary material such as this to the species level, mainly because the osteology of extant species is so poorly known that we cannot assess the diagnostic value of whatever characters are preserved in the fossils. Species like *Sindacharax lepersonnei* and *Lates rhachirhinchus* are exceptional, either because the structures involved (teeth) have been better studied or because the osteology of extant species is well known, as in *Lates*. Thus, it is quite likely that the other species represented in these collections, for example the several catfishes, may be equally distinctive when compared with their living congeners or with extinct species from other localities and times.

With this reservation in mind, however, it is still possible to compare this collection with those from later deposits in the Edward-Albert Rift (Greenwood 1959) and from contemporary or later deposits elsewhere in Africa (White 1926; Greenwood 1951, 1972, 1973b).

Except for *Sindacharax* the Miocene fish fauna of Sinda-Mohari has a typically basic Nile–Zaire facies, basic here implying that none of the endemic or specialized genera of these rivers is represented. In this respect it is akin to the Miocene fauna of Bled ed Douarah in Tunisia (Greenwood 1973b), that of the Miocene lake once occupying part of the Lake Victoria basin (Greenwood 1951), and the Pliocene fauna of Wadi Natrun, Egypt (Greenwood 1972) where *Sindacharax* was also present. The similarity can be carried forward in time to include the Pleistocene fishes of the Edward–Albert Rift (see pp. 106–119, and Greenwood 1959).

Sindacharax, apart from its occurrence in the Miocene and earlier Pleistocene of Sinda-Mohari and the Miocene of Lake Albert, is also known from the Pliocene of Wadi Natrun and Kaiso deposits of Lake Albert, where it is represented by a species differing in several dental characters and, seemingly, in reaching a smaller size (see p. 104 above, and Greenwood 1972). Furthermore, the relationships of this genus are apparently exceptional within the entire African freshwater fish fauna of Quaternary and Recent times (p. 105 above).

Some note must also be made of certain 'absentee' elements that might be expected to occur in the Sinda-Mohari fauna and which are absent also from the Miocene of Lake Albert ; see Table I. For example, there is no indication of any species of *Hydrocynus* or *Hydrocynus*-like fish (Characidae), although this genus was present in the nearby Lower Pleistocene deposits of Kanyatsi and the Pliocene of Egypt (Greenwood 1959, 1972). Catfishes of the family Clariidae are possibly represented by a single vertebra. Clariids are definitely present in the Miocene of Tunisia (Greenwood 1973b), the Pliocene of Egypt (Greenwood 1972) and in Middle Pleistocene deposits near Lake Edward. Interestingly, clariid remains are only doubtfully recorded from the basal Sinda Beds of the Sinda-Mohari area and the Lower Pleistocene of Kanyatsi (Lake Edward).

No member of the Cyprinidae, for example *Barbus* or *Labeo*, is represented in the Miocene of Sinda-Mohari nor, for that matter, in the Pleistocene beds of this area, but cyprinids are present at Wadi Natrun (two genera, Greenwood 1972) and probably Tunisia (Greenwood 1973b). It may be significant that the earliest record of a

TABLE I

Summary of species recorded from the three major areas discussed on pp. 106-119.*

	Lower Miocene	Pliocene or earlier Pleistocene (Basal Sinda Beds)	Lower Pleistocene
Sinda-Mohari	Protopterus sp. Sindacharax lepersonnei Synodontis sp. Auchenoglanis sp. Clarotes sp. ? Clariidae Lates cf. L. rhachirhinchus	Protopterus sp. Sindacharax lepersonnei Synodontis sp. Auchenoglanis sp. Clarotes sp. ? Clariidae Lates rhachirhinchus ? Cichlidae	Clarotes sp. Lates sp. (cf. L. niloticus) Lates rhachirhinchus
Lake Albert and Nyamavi	Sindacharax lepersonnei Lates sp. L. rhachirhinchus Lates cf. L. rhachirhinchus		? Synodontis sp. ? Auchenoglanis sp. Clarotes sp. Lates sp.
Lake Edward and Upper Semliki			? Hyperopisus sp. ? Synodontis sp. Clarotes sp. Lates cf. L. niloticus ? Lates rhachirhinchu.

* The few Upper Pleistocene specimens from the Lake Edward – Upper Semliki area yielded Lates cf. L. niloticus and a cichlid, probably Sarotherodon sp.

cyprinid in the Edward–Albert Rift is from Middle Pleistocene deposits at Katanda (Greenwood 1959).

Too great an emphasis should not be placed on these 'absentees' since their apparent absence could well be an accident of preservation and collection, and not due to biological or distributional factors. Nevertheless, we are impressed by the paucity of Clariidae because these fishes are abundant in mid-Pleistocene deposits in this area, and even in Pliocene deposits of Egypt (Greenwood 1959, 1972). Clariid remains are common in the Miocene Bled ed Douarah formation of Tunisia but nothing definitely clariid was found in the Miocene beds of Sinda-Mohari, and possible early Pleistocene records for this area are of only a few bones whose identity, even familial, is doubtful (see above, p. 112). As no clariid remains were recovered from the Miocene beds of Rusinga Island (Kenya waters of Lake Victoria), the earliest positive East African record for the family is, therefore, the Lower Pleistocene of Olduvai (Greenwood & Todd 1970).

This absence of clariids from East African Tertiary and some earlier Quaternary deposits, contrasted with the abundance of clariid material from later deposits here and earlier ones in north Africa, and taken together with the known ecological tolerance of extant species, may perhaps suggest that clariids had not reached the lower latitudes by that time (see also Greenwood 1973b).

Basically the same arguments could be applied to the Cyprinidae (Greenwood 1972, 1973b) although these fishes show less ecological tolerance than the Clariidae, and their later fossil record is less complete.

Unfortunately we cannot be certain about the specific identity of the *Lates* remains from the Lower Miocene of Sinda-Mohari (p. 107), but there are indications that the bones were derived from *L. rhachirhinchus*, the endemic and specialized species so characteristic of earlier Pleistocene beds in this area (see above, p. 109).

Lower Miocene collections from the Lake Albert area (pp. 115–116 and Table I) are generically more depauperate than those from Sinda-Mohari, although *Sinda-charax* is present and there is a strong suggestion of *L. rhachirhinchus* also being present. No Miocene material was obtained from the Lake Edward and Upper Semliki region of the rift.

The Pliocene or earlier Pleistocene fishes of Sinda-Mohari are essentially like those of the Lower Miocene. *Lates rhachirhinchus* is definitely present, possibly as the only species although not all the *Lates* material can be identified to species. The bagrid catfish *Auchenoglanis* is represented in the early Pleistocene collections, and there are fragments which may be attributable to a clariid catfish (p. 108).

Lates rhachirhinchus persisted in the Sinda-Mohari area until a little later in the Pleistocene (Villafranchian), and may also have done so in the Upper Semliki region (p. 118). In both places at that time, however, there was another Lates species which cannot be separated, on osteological features, from the extant L. niloticus (see above, pp. 118–119, also Greenwood 1959). Lates remains from the Villa-franchian sites of Lake Albert (p. 117) cannot be specifically identified. Later material (Upper Pleistocene to Holocene) from the Upper Semliki-Lake Edward region is certainly not attributable to L. rhachirhinchus, and the species it represents would seem to be of L. niloticus type. In other words, the temporal range of the morphologically specialized L. rhachirhinchus was, at most, from Lower Miocene to Lower Pleistocene times. Its geographical range would seem to have been restricted to the Semliki valley.

The relationships of L. rhachirhinchus, especially its apparent affinities with the present-day *Lates* species flock of Lake Tanganyika, are discussed on p. 97. For the moment no definite conclusions can be drawn as to its phylogeny, but it is clearly as derivative a species as is either L. mariae or L. microlepis of Lake Tanganyika, and certainly more so than L. angustifrons of that lake.

Until the discovery of *Sindacharax lepersonnei*, the earliest record for characoid fishes in Africa was from the Pliocene of Wadi Natrun (*Hydrocynus* sp. and *Sindacharax deserti*). It is interesting to note that these early records are all of species with a highly specialized dentition, one species (*Hydrocynus*) being undoubtedly a piscivorous predator, the other two probably specialized herbivores.

Taken in its entirety, the new material from the Lake Edward-Albert Rift throws no further light on ecological conditions obtaining during the Miocene and Lower Pleistocene, nor on the history of the fauna (Greenwood 1959). The presence of a specialized and apparently endemic *Lates* species, however, may indicate some fairly lengthy period of isolation although alternative explanations are possible (see p. 98 above). The Miocene fauna (Table I) suggests that ecological conditions at that time were probably little different from those in succeeding periods. In no period can the known fish fauna be used to decide whether the environment was that of a lake or a river. The presence of *Lates* may be taken to exclude the possibility of widespread swamp conditions because extant members of this genus are all restricted to welloxygenated water.

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